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THE RÔLE OF FLORAL ANATOMY IN THE SOLUTION OF MORPHOLOGICAL PROBLEMS

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[1] This work was done at the Botany Department, Cornell University, Ithaca, N. Y., while the author was on sabbatic leave in U.S.A. He is thankful to the university authorities for extending to him the facilities and privileges as a Resident Doctor during 1949–50.

INTRODUCTION

Notwithstanding the fact that many earlier investigators (79–82, 110, 125, 148, 170, 264, 294–297, 443) made use of vascular bundles in the interpretation of flowers, van Tieghem (451, 458, etc.) is generally regarded as the founder of the study of floral anatomy. It was indeed he who recognized this as a fruitful branch of study and through his extensive researches raised it to a place of distinction. The school of van Tieghem in France, followed by that of Eames in America and the researches of Saunders and Arber at Cambridge, have given this anatomical method the distinction which appears to be its due. As a result of active work at these centers and elsewhere, a considerable amount of literature has accumulated and claims have been advanced, time and again, that the arrangement, number, disposition and behaviour of vascular bundles provide significant and reliable clues to the puzzling variations in the external form of floral structures. It is with the idea of evaluating these claims of usefulness of this method of study in the solution of morphological problems connected with the flower that this review is undertaken.

HISTORICAL

In studying flower morphology earlier workers after Goethe (160) relied entirely upon external form. Their brilliant achievements demonstrated how much the comprehension of the flower could be advanced without reference to internal structure. Very soon, however, it became apparent that this method of investigation had yielded the best it could and that further progress depended upon study of internal structure. This was realized, probably for the first time, by Mirbel (294–296) and later by Brown (79–82) who turned to the microscope for further information. Brown's anatomical observations did not attract any attention for long, described as they were in the midst of papers largely occupied with other matters. This is perhaps the reason why they escaped the notice of Grélot (168) who gives an excellent historical review of the literature up to his time. Subsequent workers (110, 125, 148, 170, 264, 297, 433), too, did not pay whole-hearted attention to this method of study and continued to use it only casually.

The later half of the nineteenth century was a period of great

significance in botanical history. While Schleiden (389) [2], Payer (316) [2] and Hofmeister (207) [2] were busy laying the foundations of developmental morphology, and while Masters (283) [2] was focusing attention on teratological aspects of flower study, it was time that the method of vascular anatomy in floral morphology should also have its due share of attention. With this object in view, the Academie des Sciences (Paris) announced in 1866 a subject for investigation. This was "The Anatomical Structure of the Pistil and Fruit". Van Tieghem applied himself to the task and produced in a year or so a most comprehensive and voluminous monograph on the subject which not only brought him the Bordin Prize but also demonstrated, for all time to come, the value of vascular anatomy in the study of flower morphology (451). He brought forward substantial arguments to prove the appendicular nature of floral organs, particularly of the carpels, and extended this method of study to coniferous cones as well (450). Besides the monograph which was republished in 1871 and 1875, he published a number of other papers dealing with diverse groups, e.g., Lentibulariaceae (452), Juglandaceae (453), Loranthaceae (454), Primulaceae (455), Santalaceae (456), Rosaceae (460), Cucurbitaceae (461) and certain Ranales (449, 464), and several others on general topics (457, 459, 463).

Van Tieghem's monograph, being the pioneer work of its kind, left something to be desired. This was soon supplied by Henslow who studied the vascular anatomy of the flower in a large number of families (201) and did much in consolidating and strengthening the conclusions of his predecessor. In his book (200), which is fascinating reading to any student of nature, he enunciates and discusses at some length five principles of floral variation—"Number", "Arrangement", "Cohesion", "Adhesion" and "Form"—and also applies them partially to vascular bundles.

In 1897 Grélot made another detailed study of the vascular anatomy of the flower in a number of bi-carpellary gamopetalous families. But unlike van Tieghem and Henslow he emphasized that vascular anatomy of the flower should be considered from the physiological standpoint. He was of the opinion that floral parts show great plasticity according to physiological needs, and that modification of the vascular tissue corresponds to modification of

[2] For earlier publications, see (396).

the ground tissue. This view, which was first expressed by Crüger (109) in connection with the labellum of orchids, has since been supported by Goebel (159), Thompson (428) and other critics of the anatomical method.

Subsequent publications, though not so extensive, were more intensive and covered finer details of structure. Rhoeadalean families in general, and Cruciferae in particular, figured very prominently in these researches. With the opening of this new line of attack, the age-old problem of the number of carpels in the gynaeceum of the Cruciferae and Papaveraceae came to the forefront again. Both views—the *n*-carpellary and the *2n*-carpellary, *n* standing for the number of placentae—were supported on anatomical grounds. The supporters of the former (14–16, 23, 86, 134, 265–267, 330, 333, 337–339, 412) are well balanced by those of the latter (119, 131, 132, 155, 187, 237, 242, 279, 328, 329, 355, 356, 416, etc.).

The so-called Amentiferae and their allies have also attracted some attention from floral anatomists (1–3, 46, 48, 53, 142, 238, 239, 255, 256, 276–278, 304, 395, 486, 487). The main object underlying these investigations has been to elucidate through floral anatomy the real nature of the flower, which is believed by many to be very reduced here and which has actually been shown to be so in many cases (see 484).

The Rosaceae is another family which has received considerable attention on account of the controversial nature of the floral cup (55, 61, 64, 66, 69, 214, 248, 249, 273–275, 406, 445, 446, 460, 492). How far this problem has been solved will be seen subsequently. The Compositae also have been fairly exhaustively studied (243, 244, 319–321, 399, 400, 408, 421, 434, 435), and as a result considerable information regarding the morphology of the flower has become available.

Monocotyledonous families have received comparatively little attention from floral anatomists. The reason perhaps is that either the flowers are very simple, e.g., in Liliaceae, or they are highly specialized and reduced, as in Orchidaceae, Gramineae, Cyperaceae, etc. Papers that have appeared relate to Orchidaceae (417), Cyperaceae (56, 57, 407), Gramineae (10–13, 30, 47, 252, 259, 318, 322), Pandanaceae (414), Amaryllidaceae (21, 172), Zingiberaceae (167, 426, 428), Helobeae (133, 234, 447), Palmae (68, 344), Liliaceae (93, 152, 220), etc.

There are also certain publications of a more or less general nature which deal with such subjects as evolution of the flower (22, 209), vascularization of the ovule (251) and carpel (448), and structure and evolution of the stigma (186, 211, 425) and stamen (81–83).

An important contribution to the anatomical method was made at the International Botanical Congress at Ithaca when Eames (127) advocated use of anatomical studies in resolving phylogenetic problems. Following Henslow (200) and Arber (7), he asserted that vascular bundles are more conservative than external form and as such retain valuable information about the ancestry of the flower. In another paper (129) the position of the anatomical method vis à vis the concept of so-called carpel polymorphism was cleared. Considerable attention was devoted to explain the anatomical complexities that may be brought about by cohesion and adnation. This is a standard work of considerable importance which has placed the anatomical method of floral study on a sounder and clearer basis.

Arber (22), who has been one of the most active workers in the field of floral anatomy, has, however, expressed the opinion that morphology should be kept apart from phylogeny. Although in her earlier writings (7, 8) she started with a phylogenetic outlook, her subsequent treatment of the subject became more and more factual and less speculative.

Perhaps no other individual has published so much on floral anatomy as Saunders (355–385). Her observations, which cover a vast number of families and are well illustrated, are fairly reliable, but, as is well known, her conclusions are almost always vitiated by the concept of carpel polymorphism. In some of her later writings (378, 383) she avoided a discussion of this doctrine, and they represent, perhaps, her best contributions in floral anatomy.

As most of this work has already been reviewed in one way or another during recent years (22, 40, 122, 224, 247, 484), the remaining contributions will be referred to as and when necessary. But attention should be called at this stage to the recent valuable contributions of Bailey and his associates at Harvard University (31–36, 305–307, 418–420). These workers have already collected much valuable information from different aspects of flower study in some of the most primitive ranalian families. Their ap-

proach to the study of floral morphology, unlike that of many others, is most comprehensive and is commendable for the breadth of its attack, all possible features of flower structure and general anatomy of the entire plant being used.

VASCULAR GROUND PLAN AND ITS MODIFICATIONS

TYPICAL. Before taking up the numerous modifications of the vasculature of the flower, it may be worthwhile to assume some typical vascular plan as a starting point to which all the different patterns, if possible, can be referred as a standard. As it is difficult to find a flower that may be considered typical in every respect, we may well take advantage of a hypothetical pentacyclic flower without implying any phylogenetic considerations. In this flower we have further to assume that each of the five whorls—two perianth, two stamen and one carpel—receives quite distinct vascular bundles from the stele. Each sepal receives three traces —two laterals and one median—directly from the stele, given out more or less successively. The petals and stamens also receive one trace each directly from the stele. There is no cohesion or adnation of any of the vascular traces. The remaining stelar tissue may be organized into a dissected siphonostele before giving out traces to the carpels. Each carpel first receives a dorsal bundle which is immediately followed by two ventral bundles, again arising quite independently of the former and maintaining their individuality throughout their course. If any vascular tissue remains behind in the axis, it disappears as " residual tissue ".

For practical purposes this may be referred to as a typical vascular plan of the flower. During specialization of the flower this plan, like the external form, has undergone considerable modification by way of reduction or amplification of the number of bundles, or by their cohesion and adnation. In fact, the changes which affect floral organs externally may also affect their bundles to a greater or less extent.

MODIFICATION BY REDUCTION. Reduction in the number of vascular bundles in the flower is brought about through definite loss either of organs or of bundles in an organ, or through fusion. Sometimes entire whorls, particularly of petals and stamens, are lost, but generally individual members of existing whorls disappear more or less completely. In many cases the vascular bundles

of organs disappear along with the organs. For example, in certain Leguminosae the petals have been reduced from five to one (*Amorpha fruticosa*) or none (*Petalostemum candidum*), and so have the vascular bundles (300). In some cases, however, their vascular stubs may persist in the tissue of the receptacle in positions corresponding to those of the lost organs (see 130, p. 356).

Sometimes even without loss of organs certain vascular bundles may disappear more or less completely. In the corolla of certain Compositae, for instance, the midrib bundle has disappeared completely, and the marginal bundles of adjacent petals remain fused together up to the sinuses (243, 244, 399, 408). In some cases, as in *Xanthium*, they never proceed beyond the sinuses and thus disappear without separating into their component elements, while in others they may separate only to fuse again at the tips of the corolla lobes in different pairs (130, p. 348). Again the sepals in certain Primulaceae and some others have lost their marginal bundles (200, 370, 374).

MODIFICATION BY COHESION AND ADNATION. Cohesion and adnation of vascular bundles may affect their number either in the basal region of the organs only or throughout. The commonest type of cohesion is met with in the marginal bundles of carpels. In the majority of cases these bundles, which may belong to the same carpel (in axile placentation) or adjacent carpels (in parietal placentation), arise as single bundles and, if at all, give evidence of their double nature only in the upper region of the ovary or the style where they may bifurcate. Numerous instances of this type are known in different families. Similar fusion of marginal bundles of sepals is common, as is that of marginal bundles of petals in gamopetalous corollas.

In some cases a carpel receives a single bundle which later splits into the dorsal and ventral bundles (307, 375), or the bundle may not survive at all after supplying an ovular trace, as happens in some species of the Ranunculaceae (101). It is significant to note that, while in the achenial carpels of the Ranunculaceae it is the ventral bundles which have suffered reduction, in those of the Rosaceae it is the dorsals which have met similar fate (101).

Further, the median laterals of adjacent carpels in multilocular gynaecea often remain fused together for considerable distances, as in certain crucifers (328), capparids (333), saxifrages and others

(129). Similarly the marginal bundles of adjacent sepals in a gamosepalous calyx may remain united for a shorter or longer distance (129). More often sepal marginals arise conjointly with petal medians, e.g., *Moringa* (329), *Drosera* (183) and crucifers (14). In the same way the staminal bundles may arise conjointly with the perianth bundles and in the epipetalous condition may remain fused with them for a considerable distance (231, 431). Numerous cases of these types can be cited and we shall return to some of them later.

In some cases adnation of vascular bundles of different whorls seems to have affected the sequence of divergence of the traces. In *Vaccinium macrocarpum,* for instance, the petal strands which give out sepal marginals diverge at a lower level than do the sepal medians which are adnate to placental bundles (39). Similarly in certain species of the Sterculiaceae antepetalous stamen traces arise lower than those for the antesepalous stamens (341).

The fact that cohesion and adnation can modify the vascular ground plan has long been realized (200, 458). Recently it has been reemphasized (129). There is no doubt that these have been important factors in bringing about evolutionary modifications, not only in floral organs but in their vascular ground plans as well. Some controversy has developed, however, regarding the use of vascular bundles in determining the nature of the floral cup or the outer wall of the inferior ovary. It has been claimed, for instance, that in the majority of cases these represent fused bases of sepals, petals and stamens, and the vascular ground plan is called upon to substantiate this claim (129, 357, 404, 458). As far as could be ascertained, two anatomical features have been cited to support the inference. In the first place, where fusion of organs, or parts of organs, has occurred, their respective vascular bundles have remained free to a greater or less extent, showing thereby that they are not receptacular. This has been reported, for instance, in the wall of the inferior ovary of *Vaccinium vacellans, V. corymbosum* and *Gaylussacia frondosa,* and is believed to indicate that cohesion and adnation of basal regions of sepals, petals and stamens has occurred (129). Secondly, it has been pointed out that when bundles also fuse they become free in the upper region, often by a "tangential split and not a radial division, as would be the case if these bundles were departing from the stele" (129).

Bugnon (89, 90), who has questioned this inference, believes that " the relative distribution of conductive strands in no way proves the reality of such phenomena (congenital concrescence) as van Tieghem (458) thought it did. The recent attempt of Saunders (357) to confirm this theory is tainted with analogous logical error ".

Although Bugnon's conclusions have been challenged (84), it appears to the writer that his remark regarding the use of vascular bundles in this particular case is nearer the truth. It appears to the author that in the majority of cases the bundles referred to above are foliar, and here he differs from Bugnon who considers them receptacular up to the level of their separation in *Begonia*. The question, therefore, is whether foliar bundles can still traverse receptacular tissue; in other words, are they bundles or traces[3]? We shall return to this subject in greater detail in connection with the discussion of the inferior ovary. Suffice it should be to mention here that vascular bundles may not always help us determine whether the wall of the floral cup or of the inferior ovary has been formed by zonal growth in the receptacular cortex or by adnation and cohesion.

THE NATURE OF VASCULAR BUNDLES

In a discussion of the nature of vascular bundles two questions confront us rather boldly:

a) Are the vascular bundles of an organ really more conservative than its external form?

b) Do vascular bundles trespass morphological limits?

It has often been stated that when evolution proceeds in the direction of reduction, vascular structure generally lags behind the external form and becomes diminished to a vanishing point at a less rapid rate than the surface features. Although this idea is contained in some of the earliest writings on floral anatomy (81, p. 697), it was perhaps definitely formulated for the first time by Henslow in connection with rudimentary organs. He wrote (200, p. 283): " every organ can be met with in any stage of degeneration till it has completely vanished and even when all visible trace

[3] The term "trace" is used here to denote that part of a vascular strand which traverses the cortex of the receptacle (or the ovary wall in the case of an ovular trace) before entering the organ.

is wanting, the vascular cord belonging to it may in some cases still be detected. Last of all this vanishes as well".

This idea has been further elaborated in subsequent writings (7, 52, 129, 211, 247, 312*a*, 325, 356, 369, 374, etc.), and additional support has been obtained from the phenomena of adnation and cohesion (129). As has been pointed out, it was on the basis of this aspect of floral anatomy that Eames (127) advocated rather strongly the use of anatomical method in the solution of phylogenetic problems.

Arber, who once supported this view (7, 8), has revised her opinion and is now its staunch opponent. She holds (19, p. 233) that a "rudimentary form is found to correspond to a vascular system which is equally, or even more, rudimentary; indeed an organ which retains some trace of its external form, may yet show a complete lack of vascular tissue. It thus becomes clear that we have no alternative but to discard the doctrine of the conservatism of the vascular bundle".

As the subject is controversial, let us consider in some detail the evidence upon which the conception of the so-called conservatism of vascular bundles in the flower is based. As far as could be ascertained, this evidence has been drawn from four types of sources:

a) Comparison with vegetative organs having conservative anatomy.

b) Cohesion and adnation.

c) Course of vascular bundles.

d) Occurrence of vascular rudiments or stubs where organs are obviously lost.

The conservative nature of vascular tissue in certain vegetative organs has sometimes been cited in a treatment of the conservatism of vascular bundles in the flower (247). Vascular tissue has certainly changed less in certain parts or organs of plants than in others. For example, in the Cycadales the leaves (292) and cone axes (393) develop some centripetal xylem. As is well known, this is absent from the main axes of living cycads but was present in those of the Palaeozoic Cycadofilicales. On the basis of such observations, Jeffrey (216) proposed his so-called "doctrine of conservative organs". According to this conception the leaves

and cone axes in the modern Cycadales are more conservative[4] than the axis. Following the same argument certain organs or regions of the plant body in angiosperms have also been interpreted as conservative (397).

It should be noted, however, that in all these cases the vascular anatomy of the so-called conservative organ has been compared with the anatomy of the primary axis which is considered in this particular aspect to be more advanced than its appendages or in the same organ in different geological periods. In other words, we are called upon to decide whether the vascular tissue in one organ is more conservative than that in the others. In the flower, however, our problem is fundamentally different. Here we have to decide between two aspects of the same organ and say whether one is more conservative, if at all, than the other—in anatomy or external form. We are concerned here not with the fundamental nature of the vascular tissue but with the vasculature of an organ and its form. In a treatment of the flower, therefore, any reference to the doctrine of conservative organs is not only meaningless but misleading.

Coming to the second point, numerous cases are on record (129, 369, 374, etc.) where floral organs have fused among themselves but their vascular bundles are entirely free or for part of their course. Such observations have been interpreted to support the doctrine of conservatism of vascular bundles (127, 247). For instance, it has been asserted (247) that " if the question is controversial as regards gynaeceum it cannot be denied that in the corolla or calyx, for example, concrescent members often retain their individuality in the vascular system in spite of the considerable or total loss (in the mature state) of their individuality externally in the Synphylome ". Again (127, p. 424), " where organs become fused phylogenetically, as stamens with petals, proof that the condition of epipetaly of the stamen is merely one of adnation may not be evident externally, but internally there is clear proof in the presence of independent vascular supplies to the

[4] It seems necessary to qualify this statement a little. On the basis of the information we have, we are justified in regarding these organs as conservative only insofar as their vascular anatomy is concerned and not as a whole.

two organs". It is true that in these cases vascular bundles have not been subject, as yet, to the same difficulties of space under the influence of which the organs, sepals and petals or petals and stamens, or all of them, have fused. But the fact remains that in almost all cases these vascular bundles, in their behaviour and disposition, give better display than the external form of the structural conditions possessed by their ancestors.

In some cases vascular bundles, by their peculiar course, are believed to have given evidence of a condition which may have existed in the ancestral forms but which has disappeared completely in the modern species. In *Boehmeria* (46), for instance, the ovular trace does not pass directly into the ovule but ascends the ovary wall for a short distance and then turns abruptly and descends to the base of the ovule. This peculiar course seems to indicate clearly that the ovule has descended from an original lateral position. Similar downturnings in the course of vascular bundles with similar conclusions have been reported in the formation of floral cups or inferior ovaries in a number of families (61, 64, 66, 214, 329, 394, 401, 402, 460, etc.). Here also vascular anatomy has more to contribute than the external form.

It has been asserted (52, 127, 142, 179, 247, 369, 374) that when organs have been lost phylogenetically, no remnant may be present externally, but the stubs of the vascular buhdles may survive and constitute proof of the former existence of the organs. Numerous instances of the occurrence of these stubs, particularly in relation to lost stamens and lost ovules (101, 129, 404, 480, etc.), have been reported, and they have proved to be of some value in determining the real nature of the organs. Traces to lost petals, for instance, may persist in apetalous flowers of *Aristolochia, Rhamnus* and *Quercus* (130) and of *Cytinus* (368); to lost stamens in Scrophulariaceae, Labiatae, etc. (130, 374); and to lost carpels in Caprifoliaceae (209, 477–480), Ericaceae (185), Rutaceae, Valerianaceae, etc. (130). Again in unisexual flowers, where all external traces of the lost organs have disappeared, vascular traces may still be present within the receptacle, as in Fagaceae, Caryophyllaceae, Urticaceae, etc. (130). Quite often the occurrence of these vascular stubs has been cited as strong evidence to support the doctrine of conservatism of vascular bundles. Grélot (168), however, thinks differently. He has asserted,

for instance, that " vascular bundles always either belong to or are intended for an organ externally expressed and retaining its ground tissue as well ". Evidently this view envisages the fact that vascular bundles can not exist without the organ. Similar views have been expressed by some other authors (19, 159). From the theoretical physiological point of view this appears sound, for it is difficult to argue that a vascular bundle can exist without the tissue for which it is meant. If it is a bundle of some organ, then some amount of non-vascular tissue of that organ must surround the vascular bundle to justify its description. But it must be remembered that on separation from the receptacular stele (or parent bundle) the " trace " does not enter immediately into the organ for which it is intended [5]. It has to traverse some distance in the cortex of the receptacle (or parent organ, as the wall of the ovary in the case of ovule traces). If the organ in question exists at all externally the trace may enter it as its bundle, else it may disappear in the tissue of the receptacle (or parent organ). If the latter is the case, it can not be reasonably doubted that the trace in question is meant for that lost organ, and for all practical purposes it may be regarded as a trace for that organ, even though it may never enter it.

Contrary to this there are some cases on record where no vascular rudiments exist, even though the organs are believed to have been lost comparatively " recently ". For instance, in *Amorpha fruticosa* there is only one petal in place of the " standard ", the other four being absent, while in *Petalostemum candidum* all five are absent. In both these cases the vascular bundles of the missing petals are also lacking (300). Similarly in a pentaphyllous bicarpellary flower of *Gagea fascicularis* no trace of the vascular bundles for the suppressed members was observed (220). Further, there are some cases known where floral organs exist, though in rudimentary form, without any vascular tissue (16, 19, 56, 67, 142, 201, 243, 244, 300, 403, 463).

[5] If, however, we accept the opinion of van Tieghem (458) and MacDaniels (275) that "the differentiation of a floral part begins at the point where its vascular supply leaves the stele", the position will be different. According to this conception, probably, there will be nothing that we can call a "trace", for no sooner does the bundle separate from the stele than it is supposed to enter the organ it is intended for. Apparently, therefore, there is no room here for "vascular rudiment".

Saunders views this problem from a different angle. She discusses the subject under two headings (374, p. 162–163): (*a*) "When *independent* members of a floral whorl are in process of disappearing gradually, it is very usual for the last remnants of the members to persist after the corresponding vascular bundles have been lost, as happens in the case of the fifth sepal in *Veronica*". (*b*) "When, however, the member which is disappearing as such is 'lost' through being incorporated into another whorl, or when reduction in number is the outcome of fusion or failure to segment, the vascular bundles of the missing member frequently remain. The reason for these opposite results in the two classes of cases is obvious. When reduction in number occurs as a result of suppression of an *independent* member, the only destination available for the corresponding bundle pursuing its normal course is removed; and the bundle is not developed. When reduction in number takes place by a process of incorporation or fusion, the bundle can still pursue its original course in the tissue in which it lies". After giving a few examples she concludes: "We have then incontestable proof that in some cases where reduction in number is brought about by fusion or incorporation with other structures, the vascular bundle of 'lost' members does persist". Consideration of this second point will be taken up subsequently.

In the face of such instances, comparatively few though they are, it may seem difficult to justify the use of the expression "conservatism of vascular bundles". But the fact remains that vascular rudiments do survive in quite a few cases when all traces of the external form have disappeared and as such offer useful clues to the solutions of many an important problem.

Regarding the second question, there are some cases on record which seem to indicate that vascular bundles may trespass morphological limits. A close examination of such cases, however, reveals that in almost all of them facts seem to have been wrongly interpreted.

In the Primulaceae the corolla tube generally receives ten bundles instead of the usual five. The alternating additional bundles have been interpreted as antesepalous staminodal bundles (200, p. 98[6], 369, 374, etc.). Since in the majority of cases there are

[6] Elsewhere (200, p. 43) they have been interpreted, obviously erroneously, as sepaline cords.

no staminodes in these positions, the bundles are said to divide themselves equally into the margins of adjacent corolla lobes. They are thus believed to trespass the morphological boundaries, passing from the organs of one whorl to those of another. Similar cases have been reported in certain Theophrastaceae, Sapotaceae, Scrophulariaceae and Labiatae, and in other families (374). Again, in cherry the petal bundles are believed to have supplied marginal bundles for sepals (200, p. 96). As the point will be discussed later in connection with the corolla of the Primulaceae, it should suffice to mention that we are dealing here with cases of cohesion and adnation of vascular bundles and that the bundles which pass into petals actually belong to them, each petal receiving three bundles instead of the usual one. There is, therefore, no trespassing.

It has long been known (242) that in *Matthiola* and *Cheiranthus* the main lateral bundles of the sepals are quite independent of the median bundles and are derived from petal strands. This observation has been responsible for inviting a strong condemnation of the anatomical method. Referring to this it has been asserted (95) that "Anatomical method carried to its extreme would land us in a *reductio ad absurdum* of regarding the marginal regions of the Crucifer sepals as of petal nature". Arber (14), who has observed a similar condition in several other crucifer species, also interprets the sepal laterals as wholly petaline in nature and then concludes that "vascular bundles are perfectly capable of disregarding morphological boundaries".

Such strong condemnation of vascular bundles from eminent morphologists of high standing is impressive, but it is not difficult to see that these authors have based their criticisms on false premises. There is, for instance, little justification to suppose that the bundles from which sepal laterals are derived are petal bundles, as both these authors have done. In fact, it appears to be a case of adnation where bundles arising very close to each other or in the same sector often remain united for shorter or longer distances; this is known to be quite common in many families (329, 334, etc.). Each "petal strand", therefore, is actually composed of a petal midrib bundle and two sepal laterals. Arber's only difficulty in accepting this interpretation, which she envisaged herself, is perhaps that the laterals and medians of sepals arise too

far apart. In some cases the three traces of a sepal may arise from three different gaps (129).

Saunders (369, 383) has also reached the same conclusion as far as the condition in the Cruciferae is concerned. But in general she accepts the conclusion of Arber (14) to explain coloration of the monochlamydeous perianth leaves. For instance, in certain Sterculiaceae and other genera where there is only one perianth whorl she admits that the "petal" bundles divide into two branches each, which pass out as laterals into the margins of adjacent sepals. Other cases of this type have been reported subsequently (370). But here also, as has been pointed out elsewhere, fused sepal laterals have been misinterpreted as "petal" bundles.

Grélot (168, p. 130) has offered a very curious interpretation of the bundles he found in the postero-lateral positions in the corolla-androecium tube of *Salvia*. Although he admits that they are in the position of staminodal bundles, he does not concede that nature to them. On the other hand, he believes that the staminodal bundles disappeared along with the staminodes (he being a staunch opponent of the doctrine of conservatism of vascular bundles) and that some petal bundles, finding these tracks unoccupied, as it were, got into them! This shows how far astray a rigid adherence to our views can take us. Evidently, as has already been pointed out (384, 470), it is a case of staminodes, together with their vascular bundles, becoming incorporated, as it were, in the corolla tube. A similar situation exists in *Amherstia nobilis*, where the tenth staminode and its vascular bundle do not separate from the corolla tube (25).

Again, some cases are known where the gynaeceum has been observed to receive a larger number of bundles than should normally enter it. These extra bundles have often been interpreted as bundles belonging to other carpels which are believed to have existed in the ancestral forms (46, 418).

Referring to a more or less similar case in *Lathyrus*, Henslow (201, p. 179) wrote: "In the formation of the pistil it may be noted that instead of there being three well developed cords for the carpels, as occur in so many plants, e.g. *Eranthus*, it is a complete circle which has to be utilized for one carpel. Cases like this cannot be interpreted to mean that traces of other carpels have

entered into the single existing carpel but rather it is the stelar bundles which have made their way into the last floral organ". Some others have also arrived at the same conclusion (305), and the present author thinks that this is the correct approach to the problem.

Ordinarily in a fused calyx or corolla the lines of fusion may be indicated roughly by the marginal bundles or their fusion products, and the vascular supplies of individual floral leaves are more or less distinct (129, 130). In some cases, however, as in *Campanula* (200), no such distinction is maintained and a netted venation is produced all over.

Cases like the perianth of *Saraca indica* are, however, interesting. The flower here has only four perianth segments that have between them, three, three, two, two, or ten vascular bundles which in a typical leguminous flower supply two perianth whorls of five each (365, 371, 383). That it is a case of bundles disregarding morphological limits is doubtful. We shall later deal with such cases in greater detail.

From what we know at the moment it appears to be clear, therefore, that vascular bundles as a rule do not trespass morphological boundaries. This feature coupled with their slowness to change in many cases makes them a fairly reliable tool if used judiciously.

VASCULAR ANATOMY AND FLOWER MORPHOLOGY

The study of vascular anatomy of the flower has yielded information which has helped us solve many intricate problems of floral morphology. It has shown that many structures are not what they appear to be or what they are commonly taken to be. It is true that the number and size of vascular bundles can be influenced to some extent by physiological necessities (58, 109, 134, 159, 168, 257, 399, etc.) and can vary to some extent in the flowers of the same species (469). But the fundamental vascular plan, which is revealed by comparative study, remains more or less unaltered and can always be of some help, provided it is used judiciously. Sometimes individual bundles also, if they form part of a general scheme, can be of some significance, but ordinarily much reliance can not be placed on each and every bundle.

In the following pages an attempt is made to bring together as far as possible all those cases in the elucidation of which a study

of vascular anatomy has been of some avail. General discussion of the morphological nature of floral organs is ordinarily avoided, as that field has already been covered in a number of recent reviews (22, 40, 122, 129, 224, 247, 484).

PEDICELS. The pedicel, like the stem, contains a ring of vascular bundles or an unbroken cylinder of vascular tissue[7]. At one time it was thought that " the rule is for the pedicel to contain—at least immediately below the flower—if the latter is pentamerous, ten more or less distinct fibro-vascular cords, five of which belong to sepals and five to petals; if it be hexamerous, there will be six cords, three for each whorl of perianth " (200, p. 7). Traces for stamens and carpels were held to branch off from these. This rule is more often broken than observed. However, in some cases some correlation may exist between the number of bundles and that of perianth parts, but it is wrong to assign them to sepals or petals at that level.

The pedicel of *Nyctanthes arbortristis* is similar to the vegetative stem in having four inversely oriented vascular bundles in addition to those forming the normal ring (147). In *Calycanthus* the pedicel contains two vascular cylinders, one (axial) within the other (cortical). But unlike that of the stem the cortical cylinder of the pedicel consists of normally oriented bundles and furnishes traces to the lowermost perianth parts (404). The upper perianth leaves and stamens and carpels receive traces from the axial cylinder.

In highly reduced flowers the pedicel[8] may receive just one bundle running through the center, as in certain grasses (30, 259), certain sedges (56, 57, 407), some composites (243, 244, 399, 408), certain unisexual flowers (140, 192) and some others (219, 226, 336).

The vascular cylinder of the pedicel in certain crucifers shows a tendency toward dorsiventral symmetry instead of the usual radial one. This is believed to be due to relatively poor develop-

[7] Nast (305) has discussed critically the various terms applied to steles in angiosperms and she has preferred to use Brebner's (1902) term "eustele". But if the stele of angiosperms consists only of leaf-traces and no cauline bundles, as Nast believes, choice of the term "eustele" may not be appropriate on account of the implications of the prefix.

[8] The term is used here in a loose sense.

ment of vascular tissue on the adaxial side of the pedicel and is interpreted to bring the pedicels of crucifers into line with petioles instead of axes (14).

In the region where floral organs are borne, the pedicel expands more or less into what is commonly called the " receptacle ". The vascular cylinder also expands and the vascular bundles increase somewhat in number, and finally traces begin to diverge. In the simplest cases vascular traces for different organs and whorls of organs arise quite independently, e.g., in *Aquilegia* (129) and some species of *Drosera* (183). In other cases various degrees of " fusion " may take place between bundles situated more or less in the same sectors. Thus in certain advanced species of *Drosera* sepal dorsals are fused with antesepalous stamen bundles, and sepal marginals are fused with petal dorsals (183). In extreme cases carpellary dorsals also may arise fused with the bundles of the outer whorls. In certain species of the Primulaceae, e.g., *Lysimachia* (120), five bundles in the receptacle are composed of five sepal dorsals plus the fused laterals of adjoining petals (in *Samolus* antesepalous staminodal bundles may also fuse with them), and the alternating five consist of sepal laterals, petal dorsals, staminal bundles and carpellary dorsals. These fusions of different bundles often make the whole situation very complex. Obviously these are results of considerable compression and zonal growth.

SEPALS AND PETALS. Notwithstanding numerous exceptions, sepals and petals have morphologically distinctive vascular supply. Whereas a sepal usually receives three traces derived from the same (105, 270, 341, 473) or different sources (223, 492), a petal generally has one. This criterion has been of some help in distinguishing between sepals and petals. Passifloraceae, for instance, were once considered as apetalous, the inner series of floral envelopes being regarded as inner sepals (see 284). But subsequent writers interpreted them as true petals (269, 284), and this view has been substantiated by a recent anatomical study of the flower (331). The apparent petals in the Caryophyllaceae have been interpreted as adaxially fused stipules of alternesepalous stamens homologous with the glands at the bases of episepalous stamens (288, 289). This claim has also been examined anatomically and it has been found to be untenable on general morphological con-

siderations (24). Further, it appears from an examination of figures of *Lychnis* (see 24) that the vascular pattern in the basal parts of the petals is not what it would be if the petals were actually formed by the fusion of two stipule-like outgrowths, as is envisaged in the view referred to above. In this connection it may be significant to note that in *Campanula* and *Lobelia* the petal dorsals are contributed by those of the sepals. As the latter pass out, two branches diverge right and left from each. Those coming from adjacent bundles fuse together on petal radii and form petal dorsals (200, p. 98). This reminds one of the way in which stipular appendages of *Galium* and related genera are supplied with vascular bundles.

Again, Cucurbitaceae and Begoniaceae have been considered apetalous and related to Balanophoraceae, Rafflesiaceae, Datiscaceae, Nepenthaceae and Aristolochiaceae (471). It is worth noting that in *Echinocystis lobata* (Cucurbitaceae), while the sepals receive one bundle each, the petals get five each (293). A detailed study of the floral envelopes of these families may well be worthwhile.

At one time the corolla in the Primulaceae was regarded as an outgrowth from the androecium (see 349). On the basis of comparative morphology and anatomy, such a view has already been shown to be untenable (199, 286, 423). An anatomical investigation of the flower of *Persea americana* has revealed that the so-called six-parted perianth is distinguishable into a three-parted calyx and a three-parted corolla (346). The four perianth segments in *Macadamia ternifolia* receive three traces each and are thus interpreted as representing sepals (191, 233).

However, as has been pointed out above, there are numerous instances where no anatomical distinction exists between sepals and petals. Monocotyledonous families are significant from this point of view. Both the outer and the inner floral envelopes have the same vascular pattern (21, 152, 201, 417, etc.). We are, therefore, justified in using the term " perianth parts " or " tepals " here. In some cases, however, some distinction exists, as in *Urginea,* where the outer and inner members, respectively, have five and three traces each (93).

Among the dicotyledons sepals having one trace each, instead of the usual three, have been reported in some cases, e.g., *Menisper-*

mum (404), *Colpoon*[9] (402), *Olea* (240), *Lycopersicum* (102), *Echinocystis* (293) and *Primula* (200, 374). The lack of lateral veins is believed to be correlated with poor development of mesophyll tissue. It is contended, for instance, that mesophyll can form procambium only when at least two cell layers exist (236). The absence of marginal veins is, therefore, considered to be due to the fact that the mesophyll in the flanks of the sepals is only one layer thick. It is significant to note in this connection that in certain species of the Cyperaceae the bristles, which are interpreted as perianth veins, are almost without any mesophyll tissue (56, 57). In some other cases, however, the vascular supply may be amplified (see 129). In certain species of the Rutaceae sepals are found to have what are called "accessory vascular bundles" (143, 467, 468). In cases of extreme reduction sepals may not have any vascular supply, as in the perianth lobes of certain Loranthaceae (388*b*, *c*, 463), Cyperaceae (56, 57), Platanaceae[10] (67, 74, 75), Fumariaceae (16, 19), Oleaceae (225) and azaleas (105).

In the same way petals also show considerable variation with regard to their vascular supply. They have been found to have marginal bundles in a number of cases, e.g., certain species of the Winteraceae (305), Degeneriaceae (418), Goodeniaceae (79), Papaveraceae (119), Theophrastaceae and Myrsinaceae (374), Primulaceae (19, 79, 120, 201), Cucurbitaceae (293) and Solanaceae (28, 79). The origin of the marginal veins varies in different cases; they may be produced by branching of a single petal trace before it enters the petal, as, for instance, in certain Solanaceae (374), or they may be derived from different sources, as in the Primulaceae and Thymelaeaceae (120). In certain species of the Compositae the midrib bundles of the petals are replaced by two marginal veins which may remain fused with those of the adjacent petals for part or whole of their course (129, 243, 244).

In certain Moraceae an interesting difference in the vascular supply to the perianth of the pistillate and staminate flowers is recorded (46): whereas the perianth of a pistillate flower receives three traces per segment, that of the staminate gets only one. This

[9] Although in earlier works (371, 382) commissural veins have been reported.

[10] Brouwer's (78) interpretation of the plane flower is apparently incorrect (see 67).

is believed to be connected with the persistence of the perianth in the female flower as a fleshy organ.

Saunders, during her anatomical studies, has come across a number of interesting cases where vascular anatomy appears to be of special value in determining the real situation. These are described as cases of "congenital concrescence" in which certain floral organs are believed to have been incorporated in others to the apparent complete loss of their individuality. It will be worthwhile to refer to some of these cases.

In *Veronica,* while some of the species are pentamerous, typical of the family, a vast majority of them have only a four-lobed corolla. In these latter species the posterior petal often has two distinct midrib bundles, and this has been considered as evidence of complete concrescence of two petals (373, 383). On more or less similar grounds the three "sepals" of *Cistus ladaniferus* and *C. laurifolius* are considered equivalent to the normal five occurring in all other species of the genus (378, 383).

The condition in *Saraca indica* appears to be more complex. It has a colored perianth of four segments. These are described by taxonomists as sepals, and petals are believed to be lacking. A study of the vascular anatomy of the flower has revealed (365, 371, 383) that here, as in the typical leguminous flower with five sepals and five petals, ten vascular bundles (Hartog, 189, observed only nine) diverge from the central cylinder at the flower base on equidistant radii which distribute themselves into four segments—3, 3, 2, 2. This observation has been made the basis for the suggestion that all ten perianth members of a typical flower are represented in the four segments of *Saraca indica* and that nothing is suppressed or missing (365, 371, 383). A more or less similar condition has been reported in Heliantheae where some of the sepals are believed to have fused completely with the corolla tube (244). The perianth segments of *Macadamia ternifolia* were also interpreted as "compound" structures, their margins being considered as petaline in origin (232). This suggestion, however, has now been withdrawn (233).

Following the same type of reasoning, an interesting interpretation has been suggested for the corolla in Primulaceae and certain Sapotaceae and Theophrastaceae (369, 374, 382, 383, 385). It is

believed to be a "compound"[11] structure in which, in addition to the petals, are incorporated more or less completely, five antesepalous staminodes. The basis for such an inference is that the marginal bundles of the petals are believed to be not actually petaline but branches of the antesepalous staminodal bundles. It is suggested that the stamens, having lost their reproductive function, reverted to a typically foliar condition with branching midrib and ultimately got incorporated into the corolla with part or whole of their vascular supply (383).

This conclusion has been challenged, and a more easily acceptable interpretation has already been suggested (19, 120). Accordingly we are dealing here with a case of adnation in which sepal medians, petal marginals and antesepalous staminodal bundles, all arising on the same sector, get fused together in their basal region. As these fused bundles diverge, sepal medians are first separated; they are followed by petal marginals and the staminodal bundles, as in *Samolus*. But in other cases there may not be any staminodal bundles at all in the fused bundle, as in *Primula* and many others where no staminodes exist, or if present they may end at the level of forking, as seems to be the case in *Steironema* (see 374, p. 131).

In the corolla of *Soldanella* (see 374, p. 134–36), although the condition has become further complicated by lobing, there is little doubt that it can also be explained without invoking the principle of incorporation.

The conception of congenital concrescence appears to have been carried too far in an attempt to explain the phenomenon of coloring in the perianth leaves of certain monochlamydeous forms (371, 374). It is stated that if a perianth member receives its vascular supply from a single bundle it is generally green[12]; but in those forms in which "the perianth members receive vascular strands belonging to both sets of radii or sectors—midrib bundles lying on what we may term the sepal radii and commissural marginal

[11] The term "compound corolla" has been used in a different sense in *Vinca* where a developmental study has revealed that the corolla tube is receptacular below and appendicular above (59).

[12] In *Boerhaavia diffusa* the perianth segments receive only one trace each, while in *B. repanda* they have commissural veins as well, yet in both species that perianth is colored (228).

bundles derived from trunk cords or from separate strands on alternate or petal radii or sectors, the perianth may generally exhibit some degree of coloring". This notable anatomical observation has been made the basis for the suggestion that in those cases where the "commissural marginal veins are present the individual tepals, though having equally the outward appearance of unit structures, are in fact structurally 'compound' (371). Thus each perianth leaf is believed to be constructed on ½ + 1 + ½ plan".

As far as the author can see, the anatomical evidence available does not support the contention that petals are present and that instead of occurring as separate entities they have become incorporated into adjacent perianth members after splitting into two each. It seems more probable that we are dealing here with true marginal bundles of the perianth leaves and not petaline bundles. The phenomenon of coloring is a physiological process which may be connected with the flow of certain factors through marginal bundles arising on petal sectors.

It is generally believed that in the Cistaceae the ordinary rule of alternation of parts breaks down with respect to probably every whorl. With regard to sepals and petals, however, this breaking down has been found to be due to a secondary effect (378). The midrib bundles of these organs, for instance, arise definitely on alternate radii, but in their outward course the petal bundles turn to one side or the other and thus complicate the internal form.

The arrangement of sepals in the Cruciferae has been of some interest. Although the lateral sepals arise lower than the median ones, they subsequently become enclosed by the latter. This situation was realized as early as 1859 (491) and was later confirmed by anatomical study (200). It was shown, for instance, that the traces for the lateral sepals are the first to diverge from the central stele. Notwithstanding this, subsequent authors (95, 135) continued to regard the apparently outer sepals (the median ones) as really outer, and this viewpoint has appeared in many textbooks. Recently the earlier anatomical evidence for regarding the lateral sepals as really outer has been confirmed, and a mechanism has been discovered by which the median sepals get pushed out upward (14).

This interpretation was later challenged and the suggestion made that all four sepals constitute one single whorl (370, p. 177). The

early departure of the midrib bundles and the early exsertion of the lateral sepals are believed to be adaptations to provide the necessary space for the usually larger nectaries in the lateral quadrants. This, however, does not alter the fact that the lateral sepals are the outermost; the manner in which they have come to occupy that position is a separate question.

The labellum in the Orchidaceae was at one time regarded as a compound structure formed by the fusion of some staminal members with the posterior petal (81, 110). Subsequent investigators, however, interpreted it as a simple structure consisting of only one petal (109, 136, 156, 178, 287, 490). This interpretation, which was based partly on anatomy and partly on morphology, has now been confirmed by a detailed anatomical study (417). It has been shown that the vascular plan of the labellum is fundamentally similar to that of the other perianth segments and that staminodal traces have nothing to do with it.

The flowers of the Compositae have attracted the attention of morphologists and anatomists from very early times (79, 169, 201, 243, 244, 319–321, 399, 400, 408). Anatomical studies have certainly contributed a great deal toward a better comprehension of their morphology. Anatomical study of the flower has confirmed the occurrence of three types of corollas in this family—tubular, ligular and bilabiate (243, 244, 399)—and it has been indicated that the ligulate corolla is derived as a modification of the tubular corolla and not by way of the bilabiate. Further, a number of interesting features have been brought to light in the tribe Heliantheae. In certain forms here the calyx and corolla are believed to have become fused to the top of the tube. This is indicated by the occurrence of a median bundle in each corolla lobe. In such cases, therefore, the pappus can not be regarded a modified calyx. It is rather considered as a whorl of emergences (trichomes, bristles, or scales, etc.) arising from the tips of a gamosepalous structure, particularly on the posterior side (243, 244, 399, 400).

Sepals in many species of *Passiflora* end in a pointed more or less hook-shaped corniculus. This structure has been interpreted as equivalent to a petiole (184, 284). A recent anatomical study (331) reveals that its vascular pattern also is similar to that of a petiole. This has been made the basis for the suggestion that there exists a close parallelism between sepal blade and corniculus,

on the one hand, and leaf sheath and petiole, on the other. It has been further suggested that sepals and petals in *Passiflora* may have been like double-bladed organs having bifacial anatomy. Sepals in *Passiflora racemosa* show that pattern in their extreme bases (331).

Regarding the morphological nature of these organs, it may be stated that the sepals have often been considered as equivalent to bracts and foliage leaves (5, 22, 350). As has already been pointed out (129), such a view, on the whole, is borne out by a study of vascular anatomy which reveals practically the same vascular pattern as exists in foliage leaves and bracts of the same plant. The evidence in the case of the petal, however, is not so convincing, although in the majority of cases, in view of its morphology and anatomy, it is believed to have been derived through sterilization of the stamen (430, 439, etc.). From this point of view it may be of interest to note the variation in the perianth lobes of *Caltha*. In this case the perianth leaves generally receive three traces each. Sometimes some of them may have only two, owing to suppression of the third. And in a few cases the uppermost sepal, which is very small, gets only one (403). This seems to indicate yet another way in which a petal can be obtained, at least from an anatomical point of view, but morphologically this appears to be rather improbable. Again in *Menispermum* all members of the calyx, corolla and androecium receive only one trace each (404). Whether this similarity does or does not bespeak morphological affinities is not easy to determine.

The so-called "perianth" in *Lophophytum* and *Helosis* (Balanophoraceae) has been interpreted as a prolongation of the ovary (135). The same interpretation has been applied to the "perianth" in *Thoningia* (140), and it has been shown that even after the flower has become fully developed, the perianth-like limb increases in width, especially at the base, and the mouth becomes constricted and covers up the persistent lower portion of the style.

A search for the cause of delayed development of sepals in *Sherardia arvensis* has revealed that the "calyx" here is composed of spurs borne on the upper part of the ovary. This conclusion is reached in a recent anatomical study (27).

The nature of the floral envelopes in the Adoxaceae has been of some interest. The two whorls are interpreted to represent calyx

and corolla, or involucre and calyx, corolla being absent. On the basis of a morphological study (411), the second alternative has been supported. It is likely that anatomical study of the flower may throw further light on the problem.

STAMENS. A stamen generally receives a single trace which remains almost unbranched throughout its course in the filament. In the anther region it may undergo some branching. In a few ranalian families and rarely elsewhere, as in some members of the Lauraceae (346) and Musaceae (129, 130, 426) and in bamboo (12), three traces per stamen may be present. In *Ravenala* (Musaceae) each filament is traversed by from 25 to 28 small vascular bundles, scattered as in the stems of many monocotyledonous plants. Most of these disappear as the anther is approached, and the system of central bundles alone, consisting of three or four bundles, continues into the connective (426). It is interesting to note that the broad, palmately three-vein and three-trace microsporophyll of the Himantandraceae (34), Degeneriaceae (35), Chloranthaceae (420) and to some extent of the Winteraceae (33) are not differentiated into filaments, anthers and connective, and that they bear four slender elongate sporangia that are immersed beneath the dorsal surface of the sporophyll, midway between the median and lateral veins. This compares favorably with the three-veined carpel having "dorsally" borne ovules. What morphological significance can be attached to these apparent simple structures is yet to be seen.

In some cases the structure of the androecium has become complicated through adnation and cohesion or loss of parts. A study of vascular anatomy in such cases has almost always given some insight into the correct picture of the situation, as will be evident from the following instances.

The so-called labellum of the Zingiberaceae (this is to be distinguished from the labellum of the Orchidaceae) has generally been regarded as formed by fusion of two antero-lateral staminodes of the inner whorl, while the third member is the fertile stamen (37, 316, 347, 392, 458, 475, and several other taxonomists). According to this conception the two leafy members, one on each side of the fertile stamen, represent the two staminodes of the outer whorl whose anterior member is believed to be suppressed. A recent ontogenetic study of the labellum revealed that in the

tribes Costoideae and Hedychieae [13] it consists of three parts—one median staminode of the outer whorl and two lateral ones of the inner one (426, 428). This interpretation has been confirmed in an anatomical investigation of the labellum of *Elettaria* (167). A distinct vascular bundle has been observed in the median region of the labellum, and this seems to indicate quite clearly the incorporation of the outer median staminode in the labellum. This interpretation has been challenged in an ontogenetic study of *Alpinia calcarata* (340). Since no fusion of distinct parts could be observed, it is concluded that the labellum here is a single structure. This has been used as an argument for discarding the anatomical evidence brought out in *Elettaria.* It has been argued, for instance, that we have no evidence " to take it for granted that while the rest of the labellum has ceased to exist, the vascular bundles alone have persisted ". The argument advanced above does not appear to be convincing to the present author, for we are not justified in demanding entire phylogeny being repeated in ontogeny.

The orchid flower has been the subject of a detailed anatomical study (417). Evidence has been adduced to conclude that in some cases all six members of the androecium may be present, though never more than two are fertile. In the majority of the Monandrae studied, the lateral stamen bundles of the two whorls often fuse completely for greater or shorter distance and form what have been called " compound staminal traces ". This coupled with the fact that all the stamens and staminodes are fused with the style into a " column " makes the whole situation in the family very complex.

The idea that the plant body is composed of telomes is contained in the writings of Kant (230) who as early as 1790 suggested, perhaps for the first time, that the leaf and the lateral shoot are parallel members, each with a certain equivalence to the parent plant. Subsequently the same idea was elaborated in connection with the leaf of pteridophytes (70, 421), and only recently it has been applied to the stamens (481–483) and carpels in angiosperms (211, 424, 425). This view envisages the angiosperm stamen to

[13] In an earlier ontogenetic investigation (386) it was suggested that in *Hedychium* the labellum consists of only two lateral members of the inner whorl of stamens.

have arisen through reduction and fusion from a dichotomous branch system with terminal sporangia. The filament of the stamen is considered as the basal part of such a branch system, while the connective is believed to represent the subsidiary branches to which the reflexed sporangia have become fused. Support for such a view has been obtained from a study of vascularization of the stamen in certain selected plants of the Parietales and Malvales, selected on the basis of having the so-called " stamen fascicle traces ". Each stamen fascicle trace, which is a well-developed and strong bundle, breaks up into two or more staminal traces. This anatomical feature is made the basis for the telomic conception of the stamen and is posed as a serious difficulty for the prevalent view about the nature of the stamen. However, it may be made clear here that the telome theory " does not invalidate our generally held view of the flower as an axis with highly modified and specialized leaf-like appendages [14]; we may regard the stamen, and the carpel as well, not as modified leaves but as reduced branch systems, homologous with leaves of a similar origin " (483, p. 764).

The vascular pattern of the androecium in *Persea americana* has also been interpreted to support the telomic conception (346). Some support for the same idea has been obtained from a study of ontogeny of the stamen through periclinal chimeras (353). Ontogenetic studies of other authors (60, 236), however, do not seem to support such an interpretation. Evidently, as has already been pointed out (483), the evidence thus far available for the origin of the stamen in the light of the telome theory is by no means conclusive. We need much more information before the conception can claim general acceptance. As it is, some authors have preferred to do without it for the present (see 143, 331). The results of a study of vascular anatomy of the flower in certain ranalian species (36, 420) seem to run contrary to the conception of the telome theory as applied to angiosperms. Here the median strands of all floral appendages [15], including the stamen, like those

[14] Elsewhere in the description (481, 483, 484) the current view has generally been referred to as treating the stamen as a "modified foliar organ". This is different from "specialized leaf-like appendage" which is nearer the truth (22, 129, 130).

[15] Double origin for median strands of perianth segments has also been reported in *Macadamia* (232, 233).

of the foliage leaves, arise as paired structures, and this paired condition is believed not to be the result of dichotomy of a single bundle, as the telomic conception implies, but is due to "the approximation of two distinct strands originating from two separate systems of bundles" (36, p. 222).

In *Gravillea* (Proteaceae) also double stamen traces, derived from different sources in the stele, have been observed (235), but strangely enough they have been interpreted as supporting the telome theory. Such an inference does not appear to be likely unless, of course, it is assumed that two distinct branch systems form a single stamen.

OBDIPLOSTEMONY. The alternate arrangement of floral parts is so general that any exceptions to it are invested with some interest (285). The condition of obdiplostemony, in which the outer of the two whorls of stamens is superposed to the petals, is of some consequence from this point of view, although recently it has been emphasized that it is "a matter of spatial and mechanical possibilities, rather than of morphological significance" (24, p. 345). It is interesting to note that, while the condition has been reported in several dicotyledonous families, e.g., Geraniaceae (41, 114, 201, 376), Caryophyllaceae (24, 376, 430), Oxalidaceae, Rutaceae, Zygophyllaceae, Crassulaceae and Ericaceae (376), it is, as a rule, not met with in any of the monocotyledons (376). Anatomical structure reveals that obdiplostemony can be brought about probably in a number of ways.

Perhaps the simplest method is one in which the outer antesepalous whorl disappears, leaving the next whorl opposite the petals. This is found in certain Geraniaceae (114). In *Geranium maculatum*, for instance, a study of the vascular anatomy of the flower has revealed the occurrence of a third whorl of vestigial stamen traces which lie on the same radii as the sepal dorsals. Similar conditions have been reported in *Samolus*, a member of Primulaceae (120), certain species of *Passiflora* (331), and probably in some Sterculiaceae[16] (341).

In some cases the antepetalous stamen bundles do not arise separately but are carried out conjoined with the petal midrib

[16] In an earlier work (154) it has been suggested that here is a case of pseudo-obdiplostemony being induced by vascular torsion of the staminal episepal fascicle.

bundle and in this way, as has already been suggested (376), may be brought to a position farther from the center than that reached by the independently arising antesepalous stamen bundle. Such a condition has been reported in *Pelargonium* (41) and *Lychnis* (24), and it is concluded that in these cases petals and their superposed stamens "form a unit in whorl alternation without being a unit in the morphological sense" (24). Henslow (200, p. 24) reached a more or less similar conclusion.

Saunders (376), who has devoted special attention to radial organization in the flower, has reached the conclusion "that the fundamental principle of floral construction in existing cyclic form is not solely, nor primarily, that of the alternation of successive whorls of *members* but of the alternation of successive whorls of *outgoing strands* destined to become midrib bundles of the floral members . . .". Following the concept of carpel polymorphism, this author believes (356, 368, 376) that most cases of obdiplostemony are caused by the difference in radial dimensions of the so-called "valve" and "solid" carpel. "Valve" carpels, which are believed to "balloon successfully", push the inner antepetalous stamens to the outside. Henslow explained obdiplostemony in *Geranium* on the same principle of mechanical pushing (200). But recently it has been pointed out that at least in certain species of Geraniaceae (114) such an explanation is not borne out by a study of vascular anatomy. It has been determined, for instance, that the outer stamens actually arise at a lower level than the inner antesepalous stamens, while if the explanation given above were correct, it is argued, the reverse should have happened.

DEDOUBLEMENT. The number and position of stamens in the polygonaceous flower have attracted considerable attention. It is well known that in a flower such as that of *Rheum* there are two whorls of stamens, six in an outer and three in an inner whorl. Other arrangements may be derived from this by multiplication or suppression. Payer (316) explained this peculiar difference in the number of organs in the two whorls on the basis of the so-called dedoublement. He found ontogenetic evidence to suggest that to begin with there are only six staminal primordia in two whorls, but subsequently those of the outer whorl split into two each, thus doubling the number of stamens in the outer whorl. Such an interpretation of the androecium in the polygonaceous

flower has been accepted by a number of morphologists and taxonomists (136, 171, see 258). Some anatomical evidence has recently been adduced to support the conception of dedoublement of the outer stamen in *Rumex* and *Polygonum* (215). Here sometimes one of the filaments was found to have two vascular bundles. This is interpreted to mean that this particular filament has remained undivided and that thus there are only five stamens in the outer whorl instead of the normal six. In *Dionaea,* when more than ten stamens occur, it is the traces of the epipetalous stamens which branch and supply the additional stamens (405). This may appear to support the dedoublement of the inner stamens.

The vascular anatomy of the flower of Polygonaceae has recently been studied in some detail, and as a result it is felt that anatomical evidence does not lend any support to the conception of dedoublement of the outer stamens (258). If dedoublement had taken place, it is argued, the vascular bundles would not have arisen independently from the stele, as they do. It seems, therefore, logical to agree with Schoute (390) that, while dedoublement is not improbable, its existence is far from being established.

The androecium in the Fumariaceae, particularly Fumarioideae, is by no means clearly understood. As is well known, it consists in the Fumarioideae of two lateral stamen groups or phalanges, each formed of a " dithecal " member with four pollen sacs, flanked by two lateral " monothecal " members, each with two pollen sacs. This peculiar arrangement has been the cause of some bitter controversy which has been reviewed during recent years (16, 17, 370). Arber (16), who has made a special anatomical study of the subject, has supported Celakovsky's view (95) with certain modifications. She beleives that there are " six stamens—two, which are normal and dithecal, and four, which, though reduced and monothecal are independent members and not ' half ' stamens. The lateral stamens belong anatomically to the inner whorl, but in the alternation sequence they count as one whorl with the lateral petals to which they are superposed " (16, p. 353). According to Celakovsky's original conception (95), however, the lateral stamens belong to the outer whorl.

Another view, based on that of Barnhardi (50, 51) and Wydler (491), envisages two whorls of two stamens each (362, 370). The median stamens are believed to split into two each and to

form an inner whorl, since their vascular traces diverge from the stele at a higher level than do those of the lateral stamens. As has already been pointed out (16), the splitting hypothesis does not appear to be borne out by the course of vascular bundles.

The view that there are only two stamens in the lateral positions and that the inner stamens are simply their stipular appendages (136, 162) is also not borne out by vascular anatomy (16).

Yet another suggestion has been put forward rather casually (311). The lateral stamens are believed to receive double bundles, and so they are interpreted as double structures formed by the fusion of two "monothecal" stamens. As this inference is not supported by any detailed account or diagrams, it can not be taken seriously. It may, however, be pointed out that a reference has already been made to a more or less similar inference of Hilderbrand (202) regarding the inner stamens of *Hypecoum* (17). The double bundle character is considered as "*merely a direct result of a particular mode of bundle branching associated with the superposition of a stamen to a petal*" (17, p. 169–70). Additional support for such an interpretation has been obtained from a study of certain Amaryllidaceae (21).

The androecium in the Cucurbitaceae is generally composed of three anther-bearing structures, of which two appear from their double size to consist of two stamens showing in different types various degrees of coalescence up to complete fusion, each such pair being superposed to a petal, whereas the third structure, a single stamen, stands a little out of line with another petal. The compound and simple nature of these structures is clearly borne out, in some cases at least, by a study of their vascular supply[17] (97, 382, 383; and author's unpublished data). Each double structure receives two vascular bundles; the single stamen only one. It is further suggested (383) that the stamens are antepetalous and not antesepalous as is generally believed. This claim is substantiated by reference to *Fevillea* where, in addition to the normal stamens, there is an outer whorl of staminodes in antesepalous positions. However, the anatomical evidence is not very

[17] In *Echinocystis lobata*, however, each of the three stamens receives a single trace (293). In cucumber, although "double bundles" have been observed to enter the tetrasporangiate stamens, no significance is attached to this feature, and the androecium is believed to consist of two complete and one half stamen (194).

reliable on this point, for the staminal traces are not derived from the petal midribs but from petal marginals which in turn, of course, are derived from midrib bundles.

The stamens in the Ericaceae are peculiar in a number of ways, the most striking feature being complete inversion of the anther during its growth so that the real organic apex appears at the base of the adult structure. This fact would not be obvious from a study of the mature organ, but ontogenetic and anatomical studies have given clear proof of it (103–105, 290, 291, 422). For instance, in nearly all cases investigated the vascular bundle in the anther is in the form of a hook, the distal end being turned downward in the tissue of the connective and becoming evanescent towards the apparent base of the anther.

A study of vascular anatomy seems to have revealed the true morphological nature of the sterile teeth surmounting the staminal tube in certain genera of the Hibisceae and Ureneae of the Malvaceae. They were formerly believed to represent an antesepalous whorl of stamens, but now they are interpreted as terminations of the antepetalous sectors of the tube, and the antesepalous whorl in all genera is believed to be suppressed without trace (377).

CARPELS—CLASSICAL INTERPRETATION. Being the last organ borne on the floral axis, the carpel, anatomically speaking, is the most complex of all floral organs, and it should not be surprising, therefore, that it has received the greatest attention from morphologists and anatomists. According to the classical interpretation which we owe to A. P. De Candolle (117), the carpel is regarded as a leaf-like organ folded upward, that is, ventrally, with its margins more or less completely fused [18] and bearing ovules. This conception, which was originally based on external morphology, has received strong support from the studies of vascular anatomy (18, 22, 45, 129, 201, 413, 442, 448, 451). Every part of this

[18] Ontogenetic fusion of carpellary margins has been observed in a large number of species (43, 44). On the basis of this extensive work it has been stated that the degree of fusion of the carpel margins varies from a very loose one, in which the appressed epidermal layers remain easily visible, even to the naked eye, to one in which the limits of the carpel margins can no longer be distinguished. It is further suggested that the differences are purely quantitative and that completeness of the phenomenon depends upon how early in ontogeny it begins.

statement can now be supported anatomically. The fact that it is a leaf-like organ has been amply proved by its vascular supply which is perfectly similar to that of a foliage leaf. Like the latter each carpel may receive one, three, five or more traces. It has been suggested (129, 398) that, like the primitive leaf, the primitive carpel also is a three-lobed three-veined appendage. Recent researches of Bailey and his associates seem to indicate that there exists greater correlation between leaf anatomy and that of the floral leaves, including carpels, than has been hitherto realized. In *Austrobaileya* (36), for instance, the vascular pattern in the different floral leaves and bracts is believed to be identical with that in the leaf—double median bundles. The concentric or crescent-shaped bundles in the bases of carpels in Winteraceae have been compared with the petiolar bundles in foliage leaves (305).

Further, any evolutionary modification of the vascular scheme of the carpel seems to have followed the same course as that of the foliage leaf. The three-veined primitive condition has been modified by both reduction and amplification.

Again, the folded nature of the carpel is clearly indicated by the inverse orientation of the ventral bundles or placental strands, which is typical of axile placentation. In comparatively very few cases, e.g., *Dianthus, Silene, Sedum* and *Azalea,* they are, however, reported to be normally oriented (201).

Some anatomical evidence has been obtained for interpreting the apparently terminal carpels as lateral organs. While in the majority of cases all the stelar tissue is used up in supplying the gynaeceum, some cases are on record where the residual stelar tissue may continue for shorter or longer distances beyond the level of origin of the last carpellary traces. Such a condition has been reported in *Conringea orientalis* (132), in *Prunus, Actea* and *Baukinia* (129), certain Ranunculaceae (403), certain Santalaceae (401, 402), certain Caryophyllaceae (430) and many others. In still other cases the residual vascular tissue is believed not to die out but to pass into the gynaeceum as additional bundles (305, 418) or to disappear by fusing with the strands supplying the posterior petal, as in *Amherstia nobilis* (25).

The relative size of vascular bundles in a carpel has often been of some consequence. Although generally the dorsal bundle is more prominent than the ventrals, quite often the reverse may come to be true. It was noted to be so in *Rafflesia* early in the

last century (80), and subsequently it has been noted in a number of other cases (4, 168, 200, 211, 329, 424, etc.). In some extreme cases of reduction the dorsal bundles may even be lacking (412, 420). Apparently this is contrary to what one finds in a foliage leaf, and this difference has been emphasized as an argument against the foliar interpretation of the carpel (425). As has already been pointed out (22), this is evidently connected with the ovule-bearing function of the carpel. The fact that in sterile carpels or carpellodes the ventral bundles are poorly developed and disappear very early (223, 489) lends additional support for such an inference.

In highly reduced carpels or otherwise insignificant carpels the wall of the ovary may be without any vascular tissue. In Juliani-aceae, for instance, ovaries prior to or just after fertilization are reported to be non-vascular (150). Later on, however, a few vascular bundles develop. In *Agrostis canina* the only vascular supply of the ovary is a small bundle which directly enters into the ovule (318).

As in other floral organs, vascular bundles in the gynaeceum have given reliable information regarding the arrangement of carpels. The successive departure of various traces in the Capparidaceae (333), Berberidaceae (99) and probably others is used to interpret the carpels as spirally arranged. Sometimes in such cases the uppermost carpels may be too much reduced to be easily recognizable.[19]

The classical interpretation of the carpel as presented above has been subject to numerous criticisms from different points of view. Most of them amount to simple modifications (211, 354, 356, 440, 444, 481, 483), but in some cases an entirely new interpretation has been suggested in its place (see 163–166, 180, 181, 424–427 and others). All this work has already been the subject of several good reviews during recent years (22, 40, 122, 224, 247, 284), and it should be sufficient, therefore, to state that despite severe criticism and opposition, the so-called classical interpretation of the carpel has held its own as at least the best " working hypothesis ". A better interpretation has yet to be proposed.

[19] In some capparids, e. g., *Gynandropsis pentaphylla* (337) and *Crataeva religiosa* (338, 339), they have been misinterpreted as representing merely "a secondary tissue arising out of an incomplete fusion of carpellary margins" (see 333).

MONOCARPELLARY GYNAECEA. On the basis of comparative morphology it has long been believed that a multi-ovulate carpel of the follicle type is the most primitive. This contention has been borne out by the study of vascular anatomy of the carpel. It is now generally believed (101, 129, 149, 398, 403 404) that the three-trace condition—one dorsal and two ventrals—is the most primitive and that this has been modified by both reduction and amplification. Further, the contention that evolution has progressed from multiovulate to fewer ovuled condition is also borne out by vascular anatomy (101, 129, 477, 480, etc.). In some cases some of the ovules have been seen in abortive state, and in others their occurrence is believed to be indicated by the presence of their short ovular trace only (67, 101, 403).

The contention that an achene [20] is a highly modified type of follicle seems to be borne out by the recent anatomical studies referred to above. It has been shown, for instance, very convincingly how a three-trace multi-ovulate carpel can ultimately be reduced to a one-trace (and that too a poorly developed) and one-ovuled carpel. It has been demonstrated (101) that the achenial carpels in the Ranunculaceae are more reduced than those of the Rosaceae. For instance, *Waldsteinia* is reported as having an achene with the same vascular supply as a follicle, namely, a dorsal and two ventrals. Another noteworthy difference between the achenes of Ranunculaceae and those of Rosaceae that has been brought out is that, while in the Rosaceae the dorsal bundle of the carpel has suffered reduction, it is the ventral bundles in the Ranunculaceae which have had that fate.

Amplification, on the other hand, has resulted in the five-, seven-, or more-veined condition of the carpel. This is quite similar to what has been reported for the foliage leaf (398). Either this amplification may be due to branching of the dorsal bundle, as in the Ranunculaceae (403), or the additional bundle may be derived independently (305).

Carpels in *Cercidiphyllum*, one of the Ranales, deserve some mention here. They are reported to have their ventral sutures directed abaxially, that is, away from the axis on which they are borne (188, 410, 419). This is a unique orientation of the carpel

[20] The earlier conclusion (54) to the contrary is apparently wrong.

in angiosperms and is considered a " serious, if not an insuperable, obstacle to interpreting the female reproductive structure of a single flower " (419). A study of the vascular supply of the carpel has revealed that the ventral traces of the carpel are derived from bundles situated toward the periphery of the axis, whereas the dorsal vein arises from a more centrally situated bundle or bundles (419). This rules out the possibility of any twisting or resupination, as was once suggested (212). Further, a study of the vascular anatomy also supports the contention that each carpel represents the vestige of a much reduced female flower. It has been observed (419), for instance, that there are always larger numbers of bundles at the base of a carpel than are normally required for it. There are at the moment two different explanations for the abaxial orientation of the ventral suture.

According to one (410), the ancestral female flower of *Cercidiphyllum* might have possessed at least two carpels with their ventral sutures facing each other. In each flower the particular carpel which had its ventral suture adaxially oriented in respect to the inflorescence axis disappeared during subsequent evolution, and the one which had it on the abaxial side survived.

In the other explanation (188) the similarity between the orientation of the carpel on the axis of the reduced inflorescence and that of the first bud scale of the vegetative axis is emphasized. It is assumed here that the bud scale became fertile and transformed into a carpel and that the vegetative leaf or its stipular appendage became the subtending bract of the carpel.

As has already been pointed out (419), the former of these interpretations appears to be more acceptable on account of its " directness and simplicity ".

A more or less similar condition is reported in some species of *Zygogynum* (32). Here the placental ridges are situated on the abaxial side of the locule. The ovules, however, are not attached to the dorsal region of the carpel, as was once erroneously suggested (464), but to a morphologically ventral part of a conduplicate megasporophyll that has been deflected into an abaxial orientation and thus overtops the much shortened morphologically dorsal part of the carpel.

In certain species of the Berberidaceae, although there are three carpels to begin with, the lowest of the spiral develops faster than the upper two which are thus pressed out to the periphery.

Functionally, therefore, the ovary is monocarpellary, and this interpretation is borne out by a study of vascular anatomy (99). A more or less similar condition has been reported in *Rhus* (182) and certain species of the Chrysobalanaceae (62, 63), and the present author has noticed a tendency toward that end in certain *Capparis* species.

CRUCIFER CARPELS. The condition of the crucifer gynaeceum is too well known to warrant any repetition here. The anatomical peculiarities of the placental region together with the commissural stigma and mode of dehiscence of the mature fruit have baffled morphologists for more than a century. The literature which has accumulated on the subject has been analysed by several authors in recent years (14, 15, 40, 131, 328, 355). The supporters of the old de Candollean view, according to which there are only two carpels (14, 15, 134, 330, 333, 389, 412, 458), have been well-balanced, as it were, by those who believe that the placental regions represent a second whorl of two carpels (72, 131, 132, 148, 161, 200, 237, 242, 268, 279, 328, 355, etc.). Gerber (155), who was probably the first to observe the inverse orientation of the placental bundles, went a step further to suggest that there are six carpels in the crucifer gynaeceum. The four-carpellary conception, which has been referred to as the 2-*n*-carpellary view (where *n* represents the number of placentae) (328), has also been applied to Papaveraceae (119) and Capparidaceae (131, 416). In the Moringaceae the number of carpels was considered the same as in the conventional view, but the three carpels were interpreted to be specialized like the median carpel in the Cruciferae (329).

Further work by the author (330, 331, 333) has, however, convinced him that the problem of crucifer gynaeceum, and in fact that of the rhoeadalean gynaeceum in general, does not concern the number of carpels; rather it is a matter of placentation. If we understand the placentation we shall understand the gynaeceum as well. With that objective in view it has been suggested that the parietal placentation in the rhoeadalean families has been derived from axile placentation in the ancestral forms. During this change, though the margins of the carpel have moved outward, their marginal bundles have somehow retained their ancestral condition of inverse orientation and have produced inverted placental strands. Significant clue for such an interpretation has been offered by a study of *Crataeva religiosa* (333), a member of the

Capparidaceae. In this case not only is the placentation axile in the basal region but the vascular scheme also is typical for axile placentation. It is significant to note that in certain Capparidaceae and some Papaveraceae the placentation is still axile. The Cruciferae and Moringaceae, which appear to be more specialized, have lost that feature altogether, though retaining still the inverted condition of their placental strand.

This interpretation has been applied to the rhoeadalean families in general and also to the Passifloraceae (331) and Cucurbitaceae (334).

CARPEL POLYMORPHISM. The so-called theory of carpel polymorphism, which was enunciated to explain the crucifer gynaeceum, was applied with great vigor but little success to almost all angiosperm families (Saunders, 1923, and subsequent papers). It must be pointed out that the idea of carpel polymorphism is a very old one. It was perhaps first conceived by Bauer (see 82) early in the last century. Bauer suggested, probably on grounds similar to those of Saunders—one bundle for each carpel—that in the Orchidaceae there were six carpels instead of the usual three; the outer three were believed to be sterile and the inner three fertile bearing the placentae. This idea was later supported by Lindley who also applied it to the crucifer gynaeceum perhaps for the first time in 1827 (268). Kerner and Oliver (237) developed the same idea still further and applied the interpretation more generally to a number of families. They definitely recognized that "two kinds of carpels take part in the formation of many ovaries, i.e. an outer series, destitute of ovules, forming the ovarian cavity and an inner, ovuliferous series, variously metamorphosed into cushions, strings, ridges, etc.". The umbellifer gynaeceum was also interpreted as consisting of ten carpels arranged in two whorls of five each (280).

If only Saunders had realized the fate of these earlier suggestions and if only she had not put too much faith in her own premises, we should have been spared the energies of one so zealous and so enthusiastic, as also the valuable pages of esteemed journals, for something better.

More or less detailed criticism of the theory of carpel polymorphism has been the subject of many papers (19, 40, 85, 86, 129, 149, 167, 211, 224, 227, 301, 313, 484, 489, etc.). It will

serve no useful purpose to go into details again. Suffice it should be to mention here that during a life of twenty years the concept of carpel polymorphism of Saunders could receive just casual support of only a couple of workers (123, 157). It was thus more or less a personal affair with Saunders.

One point, however, must be added here, and it is this. While not agreeing with her interpretation we have to admit that her observations on vascular anatomy, which are very extensive and cover numerous families, are fairly reliable, and we can certainly take advantage of them. Moore (298), by analysing her data on the Rutaceae, has clearly shown how it can be done.

INFERIOR OVARY. The nature of the inferior ovary has been one of the most debated subjects in floral morphology for over a century. The voluminous work which has thus accumulated during this period has recently been the subject of an admirable and comprehensive review (122). All the different views which have been put forward from time to time—and they are more than half a dozen—have been dealt with. It seems pretty clear from this review that it is almost generally accepted now that the internal region of the ovary is truly carpellary. The controversy then centers round the nature of the outer region of the ovary wall which by some (57*a*, 69, 123, 124, 129, 130, 153, 172, 245, 246, 264, 312, 343, 346, 357, 417, 438, 458, etc.) has been regarded as appendicular, being formed by fusion of bases of sepals, petals and stamens with the ovary wall, and by others (42, 53, 88–90, 125, 201, 229, 241, 255, 263, 281, 388, 394, 395, 401, 402, 437, etc.) as receptacular, formed by fusion of the ovary wall with the wall of the receptacular cup.

Our object here is to see how far a study of the vascular anatomy of the inferior ovary has helped us in the solution of this problem.

In some cases vascular anatomy has given convincing proof of the receptacular nature of the outer wall of the inferior ovary. In these cases the stelar tissue goes up along the wall of the "floral cup" for some distance, and the bundles which are destined to supply carpellary traces diverge at a level higher than that of the origin of the carpels. Obviously these bundles descend in the inner region of the wall to give out carpellary traces in the bottom of the cup. As far as has been determined it has been universally

accepted that in these cases the " floral cup " is receptacular, as it is traversed by stelar tissue. Such cases have been reported in certain species of the Rosaceae (61[21], 64, 66, 214, 275, 460), Santalaceae (401, 402), Cactaceae (394), Calycanthaceae (404) and in *Hicoria* (395). The " floral cup " in these cases is believed to have been formed by a process of " sinking " or " invagination " of the floral axis, which may be conceived of in the following manner. The growing apex having become inactive, growth is continued laterally in the region below the apex and vertically in the peripheral region round the apex. As a result the receptacle rises to a greater or less extent in the form of a hollow cup, carries the peripheral organs on its edge and leaves the carpels in the bottom. This intercalary growth also involves the procambial cylinder which as a result bulges out into the wall of the receptacular cup as a pouch. Obviously, therefore, the stelar bundles which have to supply carpellary traces appear to descend along the inner wall of the receptacular cup and have their xylem on the outside.

In the majority of cases observed these bundles are used up completely in supplying carpellary traces, but an interesting situation has been described in *Darbya* (401). Here some of the descending bundles continue a downward course and disappear blindly deeper in the tissue of the receptacle. They are described as " residual bundles " of the apex of the floral stem. How they have come to point downward is really difficult to understand, unless of course we assume with Smith and Smith (401) that an actual invagination has taken place. But that will lead us into further difficulties.

In other cases the opinion is considerably divided; those who believe in the axial nature of the outer wall of the inferior ovary have based their conclusions mostly on ontogenetic and histogenetic studies, while those who believe in the appendicular view have derived their support mostly from anatomical studies. Van Tieghem and Eames have been outstanding exponents of the appendicular view. On the basis of his anatomical studies Eames (128, 129) has asserted that " the inferior ovary in nearly all—

[21] Here the occurrence of recurrent bundles in *Rosa, Prinsepia, Nuttallia* and *Sorbaria* is described as due to the disappearance of inferior carpels during phylogeny.

perhaps in all—families has resulted from the adnation of the outer floral whorls to the carpels. Histological evidence of this is available, but abundant proof is supplied by the course of the bundles and the manner of their forking and splitting". Recently MacDaniels (275) has presented the case of the appendicular view very strongly while dealing with the so often controverted pome fruit of the Rosaceae. Both Eames and MacDaniels have given particularly instructive series of diagrams from Ericaceae and Rosaceae, respectively, to show how by simple adnation and cohesion of the basal regions of sepals, petals and stamens with the ovary wall the superior ovary can become inferior.

Bugnon (88–90), on the other hand, is definitely against the idea of congenital concrescence. Notwithstanding the criticism of his views (84) he holds that the relative distribution of conducting strands in no way proves the reality of such a phenomenon as van Tieghem thought it did. He supports the conception of an axial nature of the inferior ovary in *Begonia* and others.

The difference between these two opposing schools of anatomists seems to be this: while the supporters of the appendicular view consider the bundles in the ovary wall as foliar, those who believe in the axial nature of the ovary interpret them as stelar. So the point at issue, so far, seems to have been whether the bundles in the ovary wall are foliar or stelar. The present author is inclined to believe that this is no more a problem. It appears to have been proved beyond any reasonable doubt that the bundles we are dealing with are foliar (129). But still it appears to the author that this does not solve the problem of the inferior ovary. Perhaps it may never be completely solved, for it is difficult to define precisely the terms "axis" and "appendage" which have been coined to serve convenience more than anything else. The fact that they are foliar bundles does not necessarily give us a basis for interpreting the morphology of the tissue through which they pass. We know, for instance, that leaf traces may arise in stems at considerable distances below the level of the leaf, in tissue clearly not leaf tissue. A brief consideration of the problem, as it appears to the author, is, therefore, worthwhile at this stage.

A rigid adherence to the appendicular view implies among other things that vascular bundles as soon as they separate from the stele begin to traverse the tissue of the organ for which they are intended. This has been explicitly demanded in pome fruits (275)

and is based on the so-called principle advanced by van Tieghem (451) that " the differentiation of a floral part begins at the point where its vascular supply leaves the stele ". This concept involves a point of fundamental importance. It is possible to imagine that the differentiation of a floral part begins about the level at which its vascular supply leaves the stele, but insisting that it begins at that point will mean denying the existence of any cortex in the receptacle. Not only is it against our conception of exogenous origin of floral organs and the structure of the receptacle but it is also contrary to what recent work on histogenesis and development [22] indicates.

This work on histogenesis makes it abundantly clear that floral organs, like foliage leaves, are initiated by periclinal cell divisions in the peripheral layers (tunica) of the axis. Overwhelming data on the subject have accumulated with respect to leaf. In wheat only one tunica layer is present (348), and the leaf with its procambium develops from this layer. In *Vinca rosea* the stamens and carpels are intiated in the second layer of the tunica (60), while sepals and petals develop from the second and third layer (59). In many of the Compositae the leaves, bracts and floral organs are all derived from the second layer of the tunica (260). Numerous other instances of this type, particularly those dealing with foliage leaves, are on record (see 139, 396).

As far as the present author could determine there is no statement on record worth our notice where the floral leaves are indicated to differentiate just next to the procambial tissue. Some work has, however, been done on the differentiation of foliage leaves, which goes to show that leaf traces determine the leaf (108, 138, 174, 175, 324, 415). This inference, based on the observation that in these cases the traces are formed before the leaves, is controverted for *Lupinus albus* (409); but even if it is taken for granted that it is generally so, we have yet to distinguish between what determines a leaf and where a leaf actually differentiates. The recent work referred to above appears to convince the author that there is always some amount of cortical tissue of the receptacle which separates the floral organs from the central stele and which has to be traversed before the bundle can enter the organ. In fact, the term " trace " is used to denote that feature; it is a " trace "

[22] This work has been the subject of some excellent reviews during recent years (139, 145, 396).

as long as it remains in the cortex, and the moment it enters the organ it becomes a " bundle " (130). It appears, therefore, that MacDaniels (275) is not justified in basing his conclusion on an age-old observation of van Tieghem.

Further, it has been claimed that the procambium in the developing carpels of *Amygdalus* appears first in the central part of the primordium and only afterwards becomes connected with the vascular system of the receptacle by basipetal extension (77). Such a condition is reported to be quite common in angiosperm leaves (305, 320, 321, 396). If this, as seems likely, turns out to be a more general condition, it will deal another serious blow to van Tieghem's conception which forms the basis of MacDaniels' interpretation.

Our contention, therefore, is that there always exists a few layers of cortical tissue between the stele and the floral primordia; defining their exact limits is neither possible nor relevant to our consideration. And morphologists in general do not seem to question such an inference, for they generally speak of receptacular cortex (see among others 129, 130, 481). If this is accepted we are faced with yet another possibility in which a superior ovary may give rise to an inferior or partly inferior ovary. Excessive zonal growth in this cortical region, in which traces have to traverse before entering organs, may carry the floral organs to the top of the ovary. The nature of the " floral cup " or the " ovary wall " will be determined by the region which is most active in this zonal growth. There appear to be at least three possibilities:

a) It may be most active in the extreme peripheral region, involving more or less only the base of the floral organs.

b) It may be most active in the middle layers just outside the region where " procambial " tissue differentiates.

c) In extreme cases it may be most active on the inner side of the region where " procambial " tissue differentiates.

There is no doubt that the first condition will result in more or less appendicular outgrowth, as is usually the case in the gamopetalous corolla. Similarly there can be no doubt that in the third case the resulting outgrowth will be mainly receptacular, as has been shown clearly in *Calycanthus* (404), *Rosa* (214), *Pereskea* (394), certain species of the Santalaceae (401, 402) and others. However, the condition resulting from the second possibility does not seem to be properly appreciated. It was perhaps the lack of

this appreciation which led MacDaniels to argue that " if the pome flowers were in part receptacular in nature a doubling back of the stelar bundles supplying the carpels would be expected as is the case with *Rosa* and with *Rubus odoratus* " (275, p. 22). It appears to be quite obvious to the writer that even without the stelar tissue being involved in the zonal growth, the " floral cup " can still be partly receptacular and partly appendicular depending upon how much the cortex and the peripheral region of the receptacle grow. The fact that such a differential toral growth may not involve the vascular cylinder but only the cortex of the receptacle seems to be indicated by the occurrence of receptacular discs which do not have any bulging of the stelar tissue, e.g., in *Crataeva* (333).

It will be seen now that the vascular ground plan in cases (*a*) and (*b*) will be practically the same, and it will be very difficult, if not impossible, to distinguish between the receptacular and appendicular cup merely on the basis of vascular ground plan. It is true that in most of these cases the vascular bundles are appendicular instead of stelar. But an appendicular bundle has a dual character—" trace " when it traverses the cortex of the receptacle, " bundle " when it enters the organ—and we have no easy means of distinguishing where one begins and the other ends. Hence vascular anatomy alone will be of little avail in solving the problem of inferior ovary in such cases.

PLACENTATION. It is generally believed that the ovules are borne on the margins [23] of carpels and receive vascular supply from their ventral bundles. But in some of the primitive ranalian families, like the Winteraceae (32) and Degeneriaceae (35, 418), the ovules are believed to be borne on the morphological upper surface of the megasporophyll between, and receive their vascular supply from, the dorsal and ventral bodies. Actually, however, they seem to be no more so than when called " marginal ". Again, in certain species of the Butomaceae (133) and Nymphaeaceae the ovules are scattered all over the inner surface of the ovarian wall, but not attached to the dorsal bundle [24].

[23] According to Hagerup (180, 181), the placentae are not formed by the margins of the carpels; rather they are axial structures, surrounded and protected by sterile leaves, the carpels.

[24] The earlier suggestion that the ovules in *Zygogynum* (Winteraceae) are borne on the midrib (464) has been show to be incorrect (32).

Study of vascular anatomy in flowers has afforded some good clues for better comprehension of the different types of placentation. Reference has already been made to the derived type of parietal placentation in the Cruciferae, Capparidaceae, Moringaceae, Papaveraceae, Passifloraceae and Cucurbitaceae (330, 331–334). In the Apocynaceae (488, 489), Berberidaceae (99), Orobanchaceae (200, p. 62), Caprifoliaceae (209, 477–480) and Tiliaceae (474) also the parietal placentation is believed to have been derived from axile placentation [25]. It is difficult to say at this stage whether every case of parietal placentation has been obtained from axile placentation, though Joshi (224) seems to think that it has. Gundersen (176), on the other hand, believes that parietal placentation is more primitive than axile. He bases his inference on the observation that in earlier stages the ovary is unilocular and only later becomes multilocular with axile placentation. But this is not always so (488).

The parietal placentation in *Cornus* (476) and certain species of the Gentianaceae (271) is considered antecedent to axile placentation. From the primitive unilocular condition of the ovary in the Gentianaceae evolution is believed to have progressed in two directions. While in some species the placental zone has spread laterally from the commissures, involving much of the locule wall in bearing ovules, in others "placental outgrowths" [26] from the carpellary edges have protruded in varying degrees toward the center of the locule. This tendency carried to its conclusion is believed to have produced bilocular ovaries in certain genera (271).

An interesting situation has been reported in *Garcinia* where the bicarpellary gynaeceum has only two ovules, one in each loculus (327). On the basis of the behavior of the ventral bundles of the carpels it has been suggested that only two alternate margins of the two carpels proceed toward the center and form the axile placenta, the other margins becoming sterile and remaining on the periphery. Each ovule receives the vascular supply from the ventral of the margin on which it is borne (327). This is, of course,

[25] Recent work (26, 330, 333, 333*a*, 474, 477-480) seems to indicate that the distinction which is sometimes maintained between parietal placentation and axile placentation (440, 443) is untenable, there being a graded series between them.

[26] Use of the term "placental outgrowth" seems to be misleading in so far as it recalls false partition. Evidently the author (271) means that carpellary margins themselves protrude toward the center.

the usual condition. In certain Thymelaeaceae (197), Cornaceae and Caprifoliaceae (209, 478, 479), on the other hand, the single ovule receives "double" vascular supply from the ventral bundle in each margin of its carpel. A peculiar situation exists in *Juglans* where the single ovule receives its vascular supply from both placentae (48, 304) and in certain Cyperaceae where the placental supply of all three carpels supplies a single ovlue (56, 57).

Free-central placentation has long remained a most debatable subject. The controversy centers round the nature of the central column bearing the ovules, which has been interpreted both as axial (210, 254) and appendicular (120, 121). Douglas (121) has reviewed fairly exhaustively the literature concerning the Primulaceae which was the main target of controversy. The problem seems to be well settled now in favor of the appendicular view (224, 484). The main support for such a conclusion is afforded by the inverse orientation of the vascular bundles which traverse the placental column. Van Tieghem (451) overlooked this feature in the first instance and misinterpreted the central column in the Primulaceae as axial, but he soon realized his mistake and rectified it (455). Henslow (200, 201) observed these bundles to be rounded and amphicribral, features that he used to distinguish appendicular bundles from stelar bundles which, according to him, are always endarch and wedge-shaped. Dickson (120) also observed them to be amphicribral, although Douglas (121) shows them to be inverted. Heinricher (195, 196) [27] believes that the stem growing point constitutes part of the placental column. Some anatomical evidence has been obtained to support this conclusion. For instance, it has been shown (120) that in certain species of the Primulaceae vascular residuum of the central stele frequently passes up in the center of the ovule-bearing column. This shows clearly that the central region of the column is axial, while its peripheral region which bears the ovules is carpellary (see also 122, 387). A more or less similar continuation of the axis into the placental column is also reported in certain species of the Solanaceae (302) and Santalaceae (388, 388*a*).

The condition in the Caryophyllaceae is comparatively simple. Here the carpellary septa are lost, if at all, during ontogeny, and

[27] Douglas's (121) reference to this work is apparently incomplete.

in the majority of cases the mature ovary still shows in the basal region some remnants of the disappearing septa (76, 114, 120, 430).

A simple modification of free central placentation has been reported in Polygonaceae (258). Here the uni-ovulate condition is believed to have been derived through reduction from a multi-ovulate stage with free central placentation. It is further believed that the base of the cavity is not the base of the ovary which has become solid for one-third of its height, and the ovule which appears to occupy a basal position in the cavity is really terminal on the placental axis as in *Juglans*. The funiculus, therefore, is not the simple stalk of the ovule as in most angiosperms; rather it represents a free central placenta which is greatly reduced. The vascular supply of the region is believed to substantiate this interpretation. Joshi (221), who has seen a more or less similar condition in Amaranthaceae, suspects the "funiculus" to be a real funiculus and not a placenta.

Further reduction along the same line may give rise to what is commonly called "basal placentation" with a single ovule attached in the base of the ovary. Anatomical studies have shown very clearly that the basal position of the ovule is a derived one. Definite indications still exist in certain families, e.g., Ranunculaceae (101, 129, 403), Urticales (46) and Platanaceae (67), which go to show that the basal ovule has descended from a higher position. That it may have evolved either from axile or free central placentation, as in Cyperaceae (57, 407), Compositae (49) and certain Santalaceae (401, 402), or from parietal placentation (these are not typically basal), as in Gramineae (57), Ranunculaceae (101, 129, 403), Urticales (46), Platanaceae (67), etc., is also indicated. It may be that in certain cases the axis may continue in the center of the placental column as is believed to be the case in *Osyris* (388) and certain Primulaceae (120, 195, 196), but the tissue which produces and bears the ovules is always carpellary.

The carpophore in the Umbelliferae has long been held as carpellary in nature (201, 297, 458). A recent anatomical study has confirmed this interpretation (213).

Ovule. Warming's classical work (472) established beyond any reasonable doubt the foliar nature of the ovule in angiosperms. In certain families, particularly Juglandaceae (255, 310, 395),

Myricaceae (238), Santalaceae (342) and Primulaceae (254), the ovule is still considered to be axial. It is true that in a case like that of *Juglans regia,* which has attracted considerable attention, ontogenetic and anatomical studies may not conclusively prove the foliar nature of the ovule, but comparative morphology leaves little doubt that it is so. Recently Blakeslee and Satina, who have made a special study of the Solanaceae through periclinal chimeras, have reached the conclusion that in *Datura* the carpels (354) as well as the ovules (352) are axial in nature. But the style and stigma are interpreted to be foliar, like sepals and petals (351), and stamens as axial (354). Apparently their conception of the carpel is different from the common one. They cite the work of some other authors on other species of Solanaceae (250, 473) in support of their interpretation.

Anatomical support for the foliar interpretation of the ovule comes from the fact that in almost all cases it receives its vascular supply from the ventral bundles of the carpel. Any departure from this general rule is believed to be due primarily to extreme reduction. In certain achenial carpels, for instance, the ovular traces appear to arise from the dorsal bundle, but comparative study has shown that the "dorsal" here is a compound bundle formed by fusion of both the ventrals and a dorsal (101, 129, 403). In certain primitive ranalian genera, however, the dorsal bundle is also known to contribute indirectly to the ovular supply (33, 306, 380).

It is perhaps only in basal placentation that the foliar nature of the ovule is not apparent, but here, too, vascular anatomy has helped us to see how this may have been brought about. In *Boehmeria* (46), for instance, the vascular supply of the single basal ovule descends from the suture of the ovary wall, showing thereby that the basal position of the ovule is a derived one. Similarly the ovules in the Juglandaceae (48, 276, 277, 453), Santalaceae (401, 402) and many others are believed to be foliar on anatomical grounds. The single ovule may receive its vascular supply either from one of the two marginal veins, as in *Platanus* (67), or from both, or, as in *Viburnum,* marginal bundles of other carpels also may contribute to the "compound" vascular supply of the single fertile ovule which though borne by one carpel is contained in the locule of another carpel that is sterile (479).

The vascular supply of the ovules of most angiosperms to about the time of fertilization is very weak. It may consist of just a small procambial strand in the raphe (see 309). This is perhaps the reason why the ovule has not figured prominently in anatomical studies. Our information about the condition in older ovules too is very meagre. Integumentary vascular bundles, perhaps for the first time, were described and figured in *Myrica pennsylvanica, Corylus avellana, Juglans regia* and *Quercus robur* (295, 296). Subsequently they were reported in *Ricinus communis* (170) and in several other plants (262, 459). The occurrence of an integumentary vascular system in *Myrica* and *Juglans* has been confirmed, and several new cases have been added from the Amentiferae (238, 239). The ovular bundle in *Davidia* divides and forms a considerable system in the young seed (208). Recently Kühn (251) has made a detailed study of the subject and reported well developed vascular bundles in the ovules of many families. They have also been reported in the ovules of certain species of the Anonaceae (106), Compositae (466), *Carica* (146), *Nyctanthes* (147), certain species of *Morus, Urtica* and *Rheum* (48), *Persica* (346) and *Moringa* (329). In view of the scattered distribution of integumentary bundles in different families it is doubtful that any phylogenetic significance can be attached to this feature. It has been suggested that their occurrence is more or less correlated with freedom of the integument from the nucellus (238).

The morphological nature of the shell of the nut in the Juglandaceae has been of some interest. At one time it was interpreted as formed of the ovary wall (71, 118, 310), but later it was discovered that in *Juglans regia* the dorsal bundles of the carpels are not included in that portion which becomes the shell of the nut (48, 453). It is, therefore, apparent that the shell represents only a part of the ovary wall. In *Hicoria pecan,* however, these bundles are included within the shell and it is thus formed of the entire ovary wall (395, 486, 487).

STYLE AND STIGMA. According to the classical view of the nature of the carpel, the style and stigma are considered to be its upper parts. This is borne out by vascular anatomy, since the vascular bundles of the carpel, usually the dorsal and the ventral, continue unhampered into the style and thence to the stigma (186,

211). In many genera, however, the ventrals do not extend into the style and stigma, and in some the dorsal does not (57, 211, 424). Sometimes distinction is made between what has been called true style—the sterile paracarpous region of a syncarpous gynaeceum—and stylodium which alone occurs in an apocarpous gynaeceum (186). On account of more or less complete adnation with the stamens the morphological identity of these structures has sometimes become obscured, but a study of the vascular anatomy has always been helpful in resolving the complexities brought about in this way. The compound nature of the so-called column or gynostegium of the Orchidaceae, for instance, which baffled earlier morphologists became quite apparent to Brown (81) and Darwin (110) who noticed in the column the occurrence of both the staminal and carpellary bundles. This interpretation, with modification regarding the number of stamens taking part in its formation, has since been confirmed by several authors (109, 156, 287, 417, 451). Some authors, however, believe that it is probably an outgrowth of the axis bearing the anthers and stigmas at the top (236, 347, 475).

The position of the single large stigmatic lobe in *Cypripedium*, which occupies a median position, is also of some morphological interest. It appears to be formed by the median carpel only and that the upper portions of the two other carpels are abortive. This is, however, far from true, as revealed by anatomical study (287). The fact that the vascular bundles of the two lateral carpels always enter the single stigmatic lobe clearly indicates that of the three stigmas the upper or median one becomes abortive, while the two lateral ones are joined into one compound lobe. This is another instance where a study of vascular anatomy has solved the morphological complexities of this highly specialized family, though the point still remains to be studied in the more specialized Monandrae.

The condition in *Aristolochia* is also interesting, owing to the degree of adnation. Van Tieghem (462), perhaps without caring to look into the anatomy of the region, expressed the opinion that in this case " the styles and stigmas are abortive and the six carpels are reduced to their ovaries. It is then the thickened connectives of the anthers, coherent laterally into a tube and covered with stigmatic papillae, which now play the part of the stigma and the style ". This was indeed a very strange explanation to have come from that eminent anatomist. Obviously its accuracy was sus-

pected (200), and subsequent investigation (201) did show that it was wrong. It was found, for instance, that the six bundles entering the gynandrous column bifurcate at the level of the insertion of the anther. The outer six branches diverge into the anthers, and the inner ones continue up the style to the base of the stigma. It was thus made clear that we are dealing here with a compound structure.

The gynostegium in the Asclepiadaceae and Apocynaceae also deserves some attention here. On the basis of a detailed study of *Asclepias* (107) it was suggested that the pentagonal disc in the Asclepiadaceae is mainly of stylar and staminal origin, and is not stigmatic as was commonly believed at that time. Support for such a conclusion is obtained partly from the prolongation of vascular bundles into the substance of the disc and partly from the fact that only a limited portion of the surface of the disc is receptive and secretory. In Apocynaceae also the gynostegium is believed to be of stylar and staminal origin (107). Although the interpretation appears to be more convincing than the one which considers the disc as stigmatic, taxonomists in general do not seem to have accepted it (151). The structure of the style in *Eugenia jambolana* is somewhat significant (343*a*). While the ovary here is bicarpellary, the style has five bundles like the style of *Leptospermum* where the ovary is pentacarpellary. This has been interpreted to indicate that the gynaeceum of *Eugenia* is still pentacarpellary in the stylar region, although in the ovary three of the carpels have apparently been lost. Similar condition has been reported in certain cucurbits (334) and as an exceptional case in *Crataeva religiosa* (333).

Commissural Stigma. Ordinarily stigmas are situated on the midribs of the carpels, and their splitting, if any, takes place along the lines of fusion of different carpels (carinal stigma). In some cases, however, e.g., certain species of the Cruciferae (14, 355), Papaveraceae (119, 366), Cyperaceae (57) and Juglandaceae (277) [28], they are situated on the ventral sutures, the splitting having occurred along the midribs of the carpels. Such stigmas have often been called commissural. At one time this "abnormal"

[28] The stigmas in *Drosera* and *Begonia* were also interpreted as commisural (356), but this has been shown to be incorrect (86, 183, 211, 88, 153) and the original claim has been withdrawn (360).

position of the stigma was regarded a serious situation which demanded some explanation, but now the occurrence of the commissural stigma no more disturbs the morphologist. It is simply regarded as due to the peculiar type of lobing of the apical region of the carpellary leaf (14, 86).

The behaviour of the vascular bundles in the style and stigma is of interest. The midrib bundles and the ventral bundles—if they continue their course beyond the ovary region—are known to bifurcate in the stylar region. Hunt (211) and Thomas (425), who have made a special study of the style and stigma, use this splitting of these bundles as evidence to support the telomic concept of a carpel. The ventral bundles are supposed to belong to the lateral branches which have fused with the median through webbing. In a few cases attention has been paid to determine the ending of the vascular bundles in the stigma (14, 232, 331, 414). It has been observed that all the vascular tissue in that region forms a cluster or plate of tracheids in transverse section. As such a condition has also been reported in leaf tips (9), this is believed to be "connected with the hindrance to further flow of sap when the distal region of the organ is approached" (14).

Additional stigmatic surface at the base of the true stigma has been reported in *Carya* (277). This is believed to be formed by the modified calyx and is referred to as "stigmatic disc". The entire genus *Sebaea* is reported to be diptostigmatic, that is to say, in addition to the apical stigma, secondary patches are borne on the styles (203). They are placed at right angles to the lobe of the apical stigma and are believed to represent the lower part of the edges of these lobes which have become separated from the apical stigma by intercalation of a non-papillate portion of stylar tissue.

Normally the style is lateral in attachment, but in certain Labiatae and Boraginaceae (261) it appears to arise from the gynobase below. This is the result of peculiar lobing of the gynaeceum into nutlets. The course of the vascular bundles shows clearly that in their nature they are in no way different from the ordinary styles.

The stylar canal, which is better described as transmitting-tissue (22), attracted some attention in recent years as a result of the suggestion that it represents modified ventral traces of carpel (218). This was shown to be incorrect and the suggestion has

since been withdrawn (224). The old view (92, 173) that the transmitting tissue is formed from the epidermis and some subepidermal elements of the inner faces of the carpellary margins, appears to be quite satisfactory (22, 224, 272).

An entirely different interpretation has been put on the style and stigma in Thompson's theory of acarpy. They are considered to be of androecial origin, and anatomical proof for this has been found in *Musa, Ravenala, Elettaria* and others (426, 428, 429). It is possible that these are cases of extreme adnation of carpellary and staminal bundles, but the situation has been further complicated by the occurrence of numerous bundles which do not resolve themselves into any definite pattern. It is true that such cases are few and confined to highly specialized families, and that they can not throw overboard the classical interpretation of the flower which has served as a useful hypothesis for a vast majority of cases. But the extensive researches of Thompson (426–429), Hagerup (180, 181) and Gregoire (163–166), though we may not agree with their views and sometimes with their observations, do caution us that we need not be too dogmatic about the classical interpretation of the flower.

ACCESSORY FLORAL STRUCTURES—NECTARY. Nectar-secreting organs in the flower have been variously described as "nectary", "floral nectary", "nuptial nectary" and "disc"[29] (141). The meaning of and use of these terms have never been very precise. As early as 1827 de Candolle remarked that there was hardly any term which was more misused in morphological literature than the term "nectary". Similarly Schleiden (389) wrote that all floral structures found in flowers, which could not be reduced to the four common forms, have been heaped together under the term "disc".

Floral nectaries have very diverse morphological nature in different plants. The earlier work in the subject has been admirably reviewed by Kurr (253). The interpretation which Kurr suggested more than a hundred years ago is essentially true today. According to him, floral nectaries might be developed from the usual floral parts of normal structure and function, as well as from sterilized sporophylls or reduced perianth leaves.

[29] Some authors prefer to spell it "disk". One spelling is derived from Latin "discus" and the other from Greek "diskos".

Some authors (162, 462[30]) have distinguished between nectaries dependent upon floral organs and those formed by the receptacle, the latter being called the "disc". But the modern tendency seems to apply the term "disc" to a more or less annular projection not necessarily nectar-bearing.

Dawson (114) has divided the secretory organs into two categories: (*a*) those cushions, glands or emergences which have secretory function and are not organs, and (*b*) those which represent secretory vestigial organs. Apparently the first category includes the receptacular outgrowths which are generally without any vascular supply. It has been determined, for instance, that in *Iris* 63% of the species studied had nectaries without any vascular supply (113). Nectaries in the rhoeadalean families have been the subject of study of many papers (14–16, 65, 83, 134, 141, 193, 311, 333). They have generally been interpreted as receptacular outgrowths, and vascular anatomy has furnished some evidence to support such a conclusion. Stoudt (416), while regarding the disc in the Capparidaceae as receptacular, interprets its vascular supply in *Capparis lobbiana as* "suggestive of a former staminal supply". In view of his final conclusion this appears to be a somewhat misleading statement.

The disc in the Rutaceae has long been considered as receptacular (316). Recently this claim was partly refuted and it was suggested on anatomical grounds that, while in *Glycosmia* and some species of *Clausena* it may be receptacular, it is generally staminodal in others (432), or in some cases it may be even carpellary (299). An investigation of the Eureka lemon, however, supports the older view (143).

A study of vascular anatomy has perhaps been more useful in elucidating the nature of the nectaries which are formed by vestigial organs.

The nature of the nectaries in the Salicaceae has long been a controversial subject. Some authors have considered these to be receptacular (98, 199); others have suggested, though hesitatingly, that they may be modified perianth (see 142). Fisher (142), on the basis of her anatomical and morphological studies of the flower

[30] Moore's (301) reference to van Tieghem's work that he "stated definitely that the disc was not of the nature of an appendage, but only an outgrowth of the receptacle" is misleading, for van Tieghem used the term "disc" in a limited sense.

of Salicaceae, concludes that they are modified perianth. She has traced the vascular supply in a number of species and found it in all stages of differentiation from very rudimentary in the most reduced species to well developed in the female flower of *Salix alaxensis* and *S. bonplandiana,* where she has traced the entire course of the vascular bundle from the time of its origin from the floral stele to its ultimate establishment within the tissue of the nectary. Referring to morphology she states: "conclusive evidence that these structures are not mere glands, as well as that their primitive function was not that of secreting honey is most strikingly afforded by the primitive, tropical species, *Salix bonplandiana, S. capensis* and *S. safsaf,* the glands of which are not only non-nectariferous in character, but also expanded and petaloid".

The disc in the Phaseoleae (Leguminosae), which forms a sheathing tube round the base of the ovary, has long been interpreted as staminodal (73, 115, 491). Such an interpretation, which was based more or less on external morphology, has now been confirmed by detailed anatomical study (301). The discs in *Laurus* (112) and *Beta vulgaris* (29) and in certain species of the Polygonaceae (137) have been interpreted the same way. In certain species of the Proteaceae the disc has been interpreted as representing a much reduced corolla (233, 235). A similar condition is known for the Ranunculaceae.

Basal parts of stamens have often developed into more or less prominent nectaries, as in certain members of the Fumariaceae. The course of the staminal bundles in such cases has clearly indicated the real morphological nature of the nectary (16, 141, 311).

Nectaries surrounding the base of the ovary in the Apocynaceae may vary from two to five and may be free or occasionally cohere to form a nearly uniform annular structure. Sometimes they resemble the carpels in general aspect, save for the fact that they do not contribute to the style. Woodson and Moore (489), who have made a special study of the family, have supported the conclusion arrived at earlier (488) that these "nectaries" and "disc lobes" are carpellodes. Evidence for such a conclusion is derived not only from comparative morphology but also from the fact that every one of the nectaries has essentially the same vascular supply —a dorsal and two ventrals—as that of a fertile carpel.

In the Solanaceae (205) and Boraginaceae (261) the disc at the base of the ovary is believed to be formed by an increased proliferation of the swollen base of the ovary. Vascular anatomy supports such an interpretation for the Boraginaceae.

The gynobase in the Boraginaceae, on the basis of anatomical studies, has been interpreted as partly receptacular and partly carpellary (261). In *Mertensia* it consists of four unequal lobes alternating with the four nutlets of the pistil. Those occurring on carpel backs are smaller, obtusely triangular and pointed, while the alternating ones are equal to, or longer than, the nutlets. A study of the vascular supply of the carpels has revealed that the dorsal bundle [31] of each carpel ascends into a smaller lobe of the gynobase, turns inward and downward, swings towards the style and finally turns abruptly to pass into the style (299). From this it is inferred that the small "hunchback" members of the gynobase are formed from the basal region of the carpels as a result of infolding necessarily accompanying the reduction of the gynaeceum, while the larger alternating members appear to be simple carpellodes devoid of any vascular tissue.

Nectaries or glands in the Euphorbiaceae have been variously interpreted. They have been considered as sepals, petals and stipules (see 179). The vascular anatomy of the "flower" in the family has been studied in detail, and it has been concluded that "the glands are fundamentally highly differentiated secondary ramular structures, the primitive function of which was not secretory" (179). Although no vascular tissue has been observed in the disc surrounding the base of the ovary, circumstantial evidence has been adduced to confirm the opinion of earlier botanists that it is calycine in nature (179).

Schoute (391), on the basis of his morphological study, however, has favored the interpretation which was first clearly enunciated by Eichler (136). According to this the involucre is to be considered as a phyllome whorl and the glands with the appendages as commissural products. It will be noted that this is different also from the interpretation put forward by Glück (158) and supported by Troll (441), that the commissural formations are real phyllomes and that the involucral bracts are interpetiolar stipules.

[31] Moore's fig. 9 (299) does not, however, show the same orientation of the carpellary dorsals as should be expected from his account.

This diversity in interpretation evidently emphasizes the highly reduced nature of the cyathium in the Euphorbiaceae.

Some multicellular but usually non-vascular structures, called "squamules", have been reported to occur along the pedicel of a number of crucifers (14). As they have also been observed occurring associated with leaves, they have been interpreted as stipular vestiges of the axillant bract, the main body of which is undeveloped.

Similar structures have also been reported to occur on the inner side of sepals and petals in certain Apocynaceae (158, 489) and Asclepiadaceae (4*a*). In some cases they have been found to possess a vascular supply derived from sepal and petal laterals. This exactly corresponds with the condition seen in foliar stipules, and hence they have been interpreted as stipular[32] vestiges of sepals and petals. Squamules in the Gentianaceae (271) and the petaloid scales in the Thymelaeaceae (197) have also been interpreted in the same manner on the basis of their vascular supply. Probably similar interpretation applies to squamules in *Halenia* (6). Glands in the Caryophyllaceae have also been interpreted as stipular parts of episepalous stamens and they have been further considered as homologous with petals which are regarded as stipules of the alternisepalous stamens (288, 289). As has been pointed out earlier, this latter part of the statement has been questioned and shown to be ill-founded (24).

The inter- and extra-staminal nectaries of the Crassulaceae have been regarded as appendages of the carpels rather than formations of the axis (485).

Corona. A corona in some form occurs in quite a number of families. Anatomical studies of the flower have contributed a great deal toward better comprehension of the morphological nature of its component parts. Notwithstanding Eichler's view (136) to the contrary, the corona in the Amaryllidaceae was long regarded as staminal (96, 159, 315, 465, etc.). On the basis of a recent anatomical study (21) it has been concluded that, while in *Hymenocallis* and *Eucharis* it is composed of the united bases of the stamens, it is of an entirely different origin in *Narcissus*. Here it is considered "as an outgrowth from the perianth tube, oriented to face the perianth, like the enations of double-bladed

[32] The earlier report that they are staminodes (488) is now withdrawn as incorrect (489).

foliage leaves" (21, p. 303). Fairly reliable support for such an interpretation is offered by its vascular bundles which are inversely oriented and face the petal.

The corolline nectaries of *Ranunculus* are generally associated with scales. It has been determined that the nectary trace, which arises ventrally from the median bundle, is inversely oriented with its xylem facing the xylem of the median bundle (20). Further, it has been pointed out that "this inverted bundle may be regarded as the trace for the nectary scale but since this trace is used up in supplying the nectary, the scale is left non-vascular in its free region. The idea that the scale is, despite its non-vascular character, an enation which follows the law of lamillar inversion is confirmed by a study of a peculiar form of *Ranunculus asiaticus,* in which a reduced nectary is associated with an outgrowth resembling a hypertrophied ventral scale supplied by a bundle of inverse orientation" (20).

Gray (162) reached more or less the same conclusion. When referring to the corolline outgrowths he wrote: "In *Sapindus* and some other Sapindaceae these ligular outgrowths or internal appendages are more like a doubling of the petal".

In some of the Boraginaceae the corolla bears some small scales either near the base or closing the throat of the tube. They were once suspected to be staminodes (269), but Schleiden (389) regarded them as mere folds from the surface of the corolla. Gürke (177) followed the same interpretation, and it has recently been shown to be correct on the basis of its vascular plan (24, 261).

Similar corolline scales have been reported in *Lychnis,* and they also have been interpreted as mere folds from the inner surface of the corolla (24). On each side of the scales are their non-vascular wings which are interpreted as stipular appendages.

The coronary structures in some species of the Asclepiadaceae have been interpreted to be outgrowths from the staminal filaments which, in some cases, have undergone some telescoping, probably under pressure of the gynostegium (4*a*).

The maximum elaboration of the corona is probably attained in the Passifloraceae, particularly in the genus *Passiflora.* It may consist of several series of elements, of greater or less prominence, which have been interpreted as staminodal (see 284), petaline (269, 389) or receptacular (190, 284). The vascular anatomy of

this beautifying apparatus has been studied in detail (332), and it has been determined that the vascular bundles, in the peripheral structures—radii, pali and also in operculum—are inversely oriented. This is considered to be a significant feature involving, as it does, a basic architectural distinction which must foil all attempts to interpret these coronal elements as receptacular outgrowths or sterile staminodes (332). They are interpreted as enations from "double bladed" sepals and petals. The annulus at the base of the flower does not have any vascular supply of its own and is interpreted as merely a folding of the receptacular surface. The limen in *Passiflora racemosa* is shown to be composed of five staminodes whose bases are fused together as also with the androgynophore. The origin and position of vascular bundles appear to justify such a conclusion. In other species, although no distinct staminodes have been observed and although the number of bundles in the limen is very large, it is believed to be staminodal.

Cupule, Involucre and Bracts. The occurrence of a cupule is a distinguishing feature of some of the so-called Amentiferae. It was in recognition of the importance of this feature that Bentham and Hooker distinguished Cupuliferae from other Classes. A more or less well-developed cupule occurs in the Julianiaceae, Betulaceae, Fagaceae and Juglandaceae. The structure and nature of this organ in different families is, perhaps, as varied as its form.

In the Julianiaceae, which is believed to be related to the Anacardiaceae rather than to the Amentiferae, the cupule is formed of coalescent bracts which surround three or four female flowers, although in only one or two of them the fruit develops (206).

The cupule characteristic of the Fagaceae is believed to be of two types between which, however, there are some transitions (206). The cupule of the *Lithocarpus* and the *Quercus* group is one-flowered and is always open; that of *Castanea, Fagus* and *Nothofagus* contains more than one flower and bursts open into a determinate number of lobes at maturity. The genus *Castanopsis* forms a transition between the two types. Regarding the morphological nature of the cupule in this family, a number of hypotheses have been advanced. While some emphasize the bracteolate character of the cupule (136, 231), others consider it to be essentially of axial nature, either as an intercalary formation

of the inflorescence appearing between the flower and its bracteoles (323) or, as appears to be more probable, as the product of the fused "secondary" or "tertiary" branches of a much reduced dichasium (53, 94, 206, 256, 345).

In the Juglandaceae each flower has its own cupule which is very different in external form and composition in different genera (206). The nature of the cupule, like that of the inferior ovary, has been much controverted. Those who believe the outer wall of the ovary to be of axial origin consider the cupule also to be mostly axial (255, 395). Manning (277), however, who at the time of writing his paper was apparently unaware of Langdon's work (355), interpreted the cupule as composed of one bract, two bracteoles and four perianth lobes. The same interpretation was offered earlier by Nast (304). With our present knowledge it seems hardly possible to decide the issue one way or the other.

The vascular supply of bracts is as variable as their form. When very rudimentary they may be without any vascular tissue or they may have one (198), three (331) or many traces (217). It has been asserted that, like other floral organs (236), bracts also are characterized by "open" venation in contrast to the "closed" one in foliage leaves (303). This is believed to be due to limitation of development, as indicated by the fact that in those parts of the foliage leaves which develop last, formation of veins remains incomplete (303). Considerable correlation between bracts and sepals has been found in different species of the Juglandaceae (277, 278). The morphological nature of the epicalyx, which was once disputed, appears to be well settled now in certain Rosaceae where it has been suggested that it consists of bracts coordinate with sepals and leaves rather than coalesced stipules of sepals (91).

A detailed anatomical study of the involucre of *Anemone* has thrown some light on the nature of this structure. Evidence has been adduced to show, for instance, that in *Anemone hepatica* it is homologous with the calyx of *Ranunculus ficaria* (100). Philipson (319–321), who has made a special developmental and anatomical study of the involucral bracts in the Compositae, has, on the other hand, found every gradation in vascular anatomy between an ordinary foliage leaf and a one-trace involucral bract. This appears to show that bracts form a transition stage between foliage leaves, on the one hand, and sepals, on the other.

CONCLUSION

It thus seems fairly clear that vascular study of the flower has made quite an honorable contribution to the solution of morphological problems. In some cases problems have actually been solved; in others their better appreciation has resulted; and solutions will follow as the frontiers of knowledge advance. Obviously, therefore, the anatomical method does not deserve the contempt with which it has been treated in certain quarters. No doubt vascular bundles depend [33] upon organs for their formation (and, shall we say, for their existence?), but once they are formed they attain some amount of autonomy with regard to their behaviour by virtue of the fact that they are not exposed to spatial difficulties to the same extent as are the organs which contain them. This makes them fairly reliable if used judiciously. The fact that in some cases too much has been claimed for vascular bundles should not scare others to the other extreme. This, however, is no pleading for anatomical method as a discrete entity. It may be emphasized once again that " this is but one aspect of form—external morphology is another and ontogeny is still another ". And none of them considered by itself is the only " way to salvation ".

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[33] Kozo Poljanski (247), however, believes that "they are mutually connected and neither is determined by the other".

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